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Feeding Behavior of the Widow Rockfish (*Sebastes entomelas*), A Diurnally Feeding Rockfish

Peter B. Adams
National Marine Fisheries Service

Introduction

Prior to 1978, widow rockfish landings were an insignificant component of the Northeastern Pacific Groundfish Fishery, but since then, these landings have grown from below 1,000 mt to an estimated 28,000 mt in 1981. This dramatic increase in the fishery has more than doubled the commercial landings of rockfish in the area off California, Oregon and Washington (PFMC 1981). Now the immediate question is how these people that are in this highly competitive business could have overlooked this vast resource all this time. There are many reasons but the principal one is that the widow fishery is fundamentally different from traditional rockfish fisheries. The traditional rockfish fishery is a daytime bottom trawl operation while the widow fishery is a nighttime midwater fishery. Obviously it is important to understand these differences in behavior of the widow rockfish (a nocturnal aggregating species) from the traditional commercially important rockfish species which aggregate diurnally. Actually this is really the converse of the question since in most fish species that aggregate into schools and disperse, it is the dispersed stage when the fish is feeding that is the driving force of this day-night cycle (Hobson 1973).

Diurnal Feeding

Stomach sample data were taken primarily from commercial landings in the Eureka area, supplemented with other samples from Northern California sport and commercial catches. Most were fish taken in the nighttime midwater fishery. The diet of the widow rockfish consists of salps, fish, (primarily myctophids) shrimp and euphausiids (Table 1). These four groups are roughly equal in the diet and make up over 90% of the total diet volume. The only other commonly occurring prey group is hyperiid amphipods. Phillips (1964) felt that these amphipods domnated the diet of widow rockfish. All these prey groups represent organisms that migrate to the surface at night while the widow rockfish is aggregated near the bottom. So probably these prey are taken during the day in their submerged stage (Adams in prep).

The obvious next step is a directed fishing effort to obtain day and night stomach samples from members of the same population. This data would be used to examine their pattern of gut fullness. This was attempted in conjunction with a NWAFC research cruise that was attempting to make biomass estimates of the widow rockfish population off Oregon. The vessel used in the cruise was the R/V Chapman, a new stern end trawler which is equipped with the most recent electronic and mechanical fishing gear, but even using this boat, we were unable to consistently catch fish in midwater. Midwater fishing is very sophisticated. Besides extensive technological gear, it requires a great deal of fishing experience plus current feedback on the local fishes' schooling behavior. It is questionable whether any research vessel, no matter how suitably equipped, can successfully fish in midwater without extensive prior experience. Nevertheless, we need this type of data to answer the day-night feeding question.

Seasonal Feeding

There are also strong seasonal differences in the diet considering just the four major groups mentioned earlier; euphausiids, shrimp, salps and fish. These four major groups dominate the diet (accounting for between 82 and 97 percent of the quarterly diet volume), but the distribution of diet volume among the four major groups is different during the year (Figure 1). During the fall, fish dominate, while in the winter, the major prey are shrimp. In the summer quarter, the widows are feeding on euphausiids and fish. The spring quarter is the only period when salps are a major part of the diet. This period and summer are the only time of the year when euphausiids are important. The spring quarter is also the period of highest absolute volume of prey per fish and also of the highest number of prey categories per fish.

This pattern is significant since the widows are feeding most heavily just after they have finished partition (release of young) during winter months (T. Echeverria per. comm.). There is a high demand for energy during reproduction, and following this activity stored energy is at its lowest level. In other species, natural mortality is concentrated during this period (Shul'man 1974), and perhaps this is also true for widow rockfish.

Discussion

Random sampling is rarely possible in feeding studies; therefore it is important to understand the relationship between different types of sampling and the error involved. How stomach samples are gathered cannot be considered independent of the intended questions that are going to be asked of that data. Samples used here were gathered both from research cruises (directed sampling) and from commercial port sampling (incidental sampling). Average values of the amount of a particular type of prey item will differ from true population values because of variation and bias. Variation is the spread (or dispersion) of the observed sampled values around the mean. The enormous variation typical of food habitat data is due largely to its patchy or contagious nature. These types of data have sampling distributions which are skewed and have a large proportion of empty sample elements. That is, it it common for a prey item to occur in only a few fish, but for those few fish to be stuffed with them. In order to evaluate the relative importance of this type of variation in both direct and indirect sampling, I looked at the degree of patchiness in a research trawl versus a commercial landing using Lloyd's (1967) mean crowding index. For the different major prey groups, the patchiness indices are very similar, with the commercial data consistently less patchy (Table 2). Essentially this means that the relationship between the mean and the variances is similar, and although neither of these data sets are normally distributed, there is not a great deal of difference in this aspect of the data between these two types of sampling.

The other possible source of error, sample bias is simply when certain individuals in the population have a greater chance of being included than others. Bias is unrelated to variation. Confidence limits can be very narrow, but still strongly biased. Bias usually results when the sample coverage of the population is inadequate in some area. In Figure 2, the large distribution is the lengths of fishes used in all of stomach samples from port sampling; the small distribution is the lengths of all widows taken in midwater hauls during the April research cruise. Even though the research cruise sample represents almost 200 fish versus around 500 for the port sampling, the range of lengths in the research survey data covers only a small portion of the length range of the port samples. Both of these samples are biased in different ways. In common usage, the term bias, in common usage, has negative connotations implying a faulty sampling design. But bias is really a problem only when it is unrecognized. Attempts to identify bias must be independent of attempts to reduce variance.

Of the two types of sampling, port sampling has the advantage of much lower costs. Incidental sampling of this sort can provide descriptive information about the target population, an example being the seasonal distribution of food of the widow rockfish. However, except in unusual circumstances, this type of data is not adequate for hypothesis testing. When data are needed to detect differences between subgroups of the target population to verify hypothesis, a directed sampling effort is needed.

The widow rockfish offers a typical example of the evolution of management of a species. Usually, a fishery develops explosively. As with the widow rockfish, usually little or no previous information is available prior to the onset of the fishery. Management plans based completely on age and growth studies are developed after intense fishing has taken place. Traditionally feeding studies had no impact on these plans. I have thought about why this is so and there are two possible reasons. The first is that feeding is an unimportant aspect of the fishes' biology. My studies and the views expressed at this workshop, indicate this is untrue. This leaves the second reason that feeding studies have failed to provide the kind of information that is necessary for management. If this is so, the obvious question is: What kind of information is needed by management?

My idea of the kind of food habit data needed for management is related to how fish communities are structured. Ecological theory concerning community structure has been dominated by the Hutchinson-

MacArthur school of thought. In its simplest form, this type of theory views a community of animals as a unidimensional resources axis upon which species occupy some area or breath. When there are multiple species, a zone of overlap exists where species co-occur. The underlying assumption of this theory is that direct competition is the principal force in determining community structure and therefore controls these patterns of niche breath and overlap. This view regards feeding studies as simply a means of identifying potential competitors. When the diets of offshore fishes are found to be widely overlapping, direct competition for food, and therefore feeding studies, is considered unimportant in management strategies. In the terrestrial communities for which these concepts were developed, this theory has been widely accepted, but in aquatic communities, predation has been found to be one of the most powerful integrating concepts (Hobson 1968; Lowe-McConnel 1975; Paine 1966). An alternative to the Hutchinson-MacArthur model is to view the community as a lattice, then the vertical connections would represent predation and the horizontal connections would be competition. Using this model, predator-prey relationships can be an important factor in community interactions. If there is ever going to be true multi-species management, feeding studies are going to have to focus more toward these vertical connections both above and below the managed species and the mechanisms which control them.

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Table 1. The diet of widow rockfish from Northern California (Average TL = 464 mm, min. Size = 361 mm, Max. Size = 543 mm, n = 365).

	Number	Volume	Min. Size	Max. Size	Freq. of Occurrence
Hydromedusae	1.28	3.90	1.00	4.00	0.06
Ctenophora	0.10	0.84	0.50	3.00	0.01
Oligochaeta	-	0.27	90.00	-	0.01
Pelagic Polychaeta	0.07	0.56	2.50	2.70	0.01
Pelagic Gastropoda	0.13	0.79	7.00	-	0.02
Cephalopoda	0.14	0.91	50.00	-	0.03
Mysidacea	0.01	0.01	1.00	-	0.01
Isopoda	0.01	0.28	1.50	-	0.01
Gammaridea	0.07	0.34	1.00	-	0.03
Hyperiidea	1.45	3.77	0.70	10.00	0.18
Caprellidea	0.01	0.01	1.00	35.00	0.01
Euphausiacea	30.88	21.05	6.00	36.00	0.37
Natantia	11.78	12.78	0.30	7.00	0.20
Ascidiacea	0.02	0.22	1.50	2.00	0.01
Larvacea	0.11	0.03	0.30	0.68	0.01
Thaliacea	22.98	16.74	1.00	80.00	0.370
Chaetognatha	0.01	0.55	-	-	0.01
Fish	5.38	24.80	1.50	90.00	0.403
Undet. Gelatinous material	-	10.22	6.00	-	0.02
Sand	-	0.91	-	-	0.01

Table 2. Lloyd's (1967) index of patchiness for major prey categories from research trawls versus commercial landings.

Prey Categories	Commercial Landings	Research Trawls
Euphausiids	2.72	2.30
Salps	3.94	1.34
Shrimp	10.15	10.36
Fish	10.71	.24

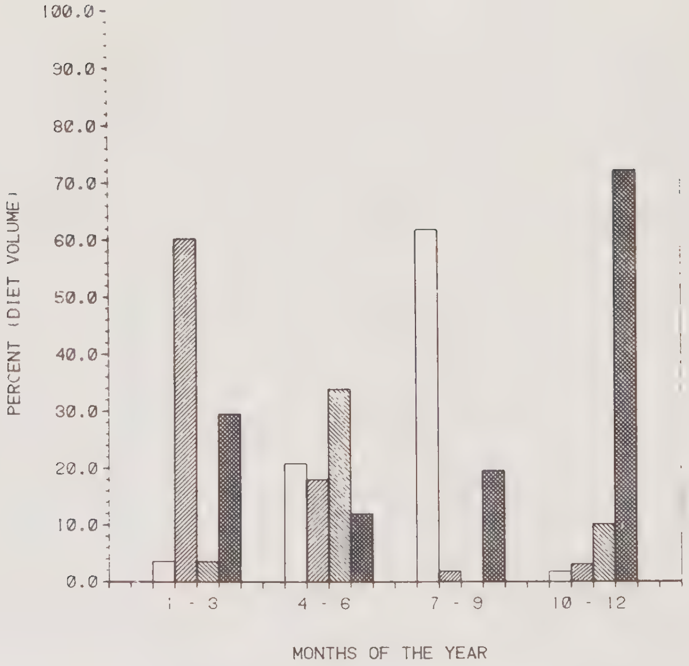

Figure 1. Seasonal feeding of the widow rockfish on salps (clear bar), shrimp (left-hatched bar), euphausiids (right-hatched bar) and fish (cross-hatched bar).

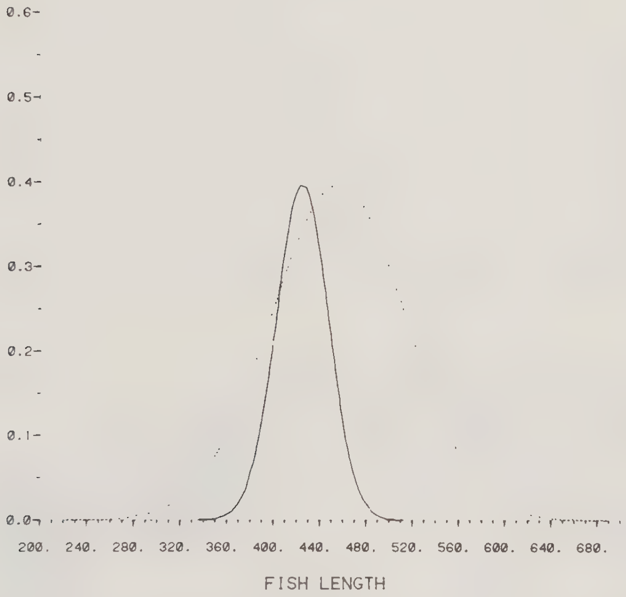

Figure 2. This distribution of lengths of widow rockfish from port sampling (dashed line) and from the April research cruise (solid line).

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MORPHOLOGY AND GROWTH OF A PUGHEADED BROWN ROCKFISH, SEBASTES AURICULATUS

During a population study on brown rockfish, *Sebastes auriculatus,* in San Francisco Bay, a pugheaded brown rockfish (Figure 1) was caught four separate times. The study, which included the taking of morphometric, tagging, and growth data, provided an opportunity to statistically test certain characteristics of the pugheaded fish against normal brown rockfish. The morphometric comparisons describe the effects of the pugheaded condition on growth of other parts of the body. Tagging data show the effects of pugheadedness on overall growth. This is the only instance known to us of a direct measurement of growth of a pugheaded fish. These data can be used to answer the question: Is this fish handicapped by its pugheadedness and, if so, how much?

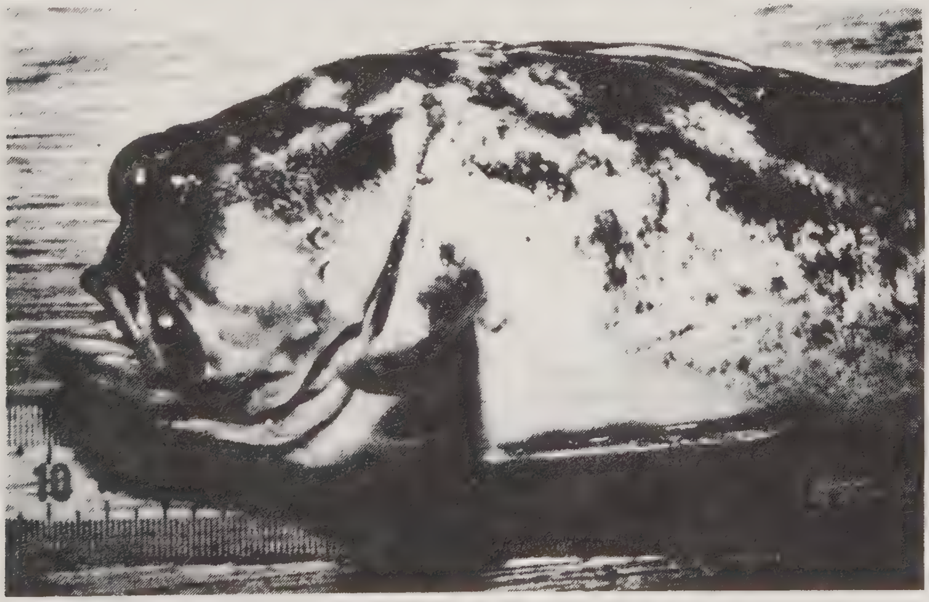

FIGURE 1. A pugheaded brown rockfish, *Sebastes auriculatus,* caught in San Francisco Bay near Tiburon, California.

Morphometrics of over 100 normal fish were regressed against total length (tip of lower jaw to the maximum length of the caudal fin). Measurement definitions were the same as those used by Phillips (1957). These regressions were used to estimate morphometrics for an "average" fish with a total length of 240 mm. The morphometrics of the pugheaded fish were compared with those of the "average" fish using *t*-tests.

The three morphometrics associated with pugheadedness—head, snout, and upper jaw lengths—were significantly smaller ($P > 0.05$) than the expected values (Table 1). The least depth of the caudal peduncle is significantly larger than expected normally. However, regression of the caudal peduncle against other parts of the body indicate that this is the result of random variations in the data. No other body parts differ significantly from those expected.

TABLE 1. Morphometrics and *t*-Test Statistics for Pugheaded and "Average" Brown Rockfish, *Sebastes auriculatus*.

Measurements	*Pugheaded fish (mm)*	*Estimated "average" fish (mm)*	*t-test value*	*Degrees of freedom*
Head length	63.5	71.5	−2.31*	109
Body depth at ventral fin	68.6	67.2	0.24	79
Body depth at anal fin	53.4	52.1	0.33	103
Length of anal fin base	29.2	29.8	−0.20	115
Length of snout	13.2	17.5	−1.73*	109
Width of orbit	16.2	17.1	−0.46	114
Width of interorbital space	12.9	12.8	0.11	106
Length of upper jaw	30.0	34.6	−2.38*	107
Width of base of pectoral fin	20.4	19.2	0.99	111
Longest pectoral fin ray	49.9	52.5	−0.78	110
Longest pelvic fin ray	37.8	41.7	−1.14	108
Length of pelvic spine	27.6	26.8	0.35	107
Length of first anal spine	15.2	14.0	0.69	107
Length of second anal spine	30.1	28.0	0.64	90
Length of third anal spine	27.1	25.9	0.48	107
Longest anal fin ray	35.7	37.5	−0.80	107
Longest dorsal fin spine	37.3	33.9	0.66	76
Longest dorsal fin ray	31.4	33.2	−0.71	94
Least depth of caudal peduncle	22.0	19.5	1.74*	77
Posterior of anus to origin of anal fin	10.4	11.2	−0.31	56

* Significant at the 95% probability level.

Body parts other than those directly stunted by the pugheadedness grew in normal proportion to each other. The orbit and interorbital space were not significantly different from normal, indicating that the pugheadedness and exophthalmic condition (bulging eye) are the results of a shortened snout and upper jaw and are not independent conditions.

During a period of 15 months, the pugheaded brown rockfish was caught four times (Table 2). The fish was double-tagged with Floy [1] T-bar tags at the first capture date. The fish has been deposited in the fish collection at the California Academy of Sciences (CAS 46146). The daily growth rates for both the pugheaded and normal fish were calculated for all of the six possible time periods (Table 3). Only those fishes caught during the same time interval as the pugheaded fish, and with total lengths between 150 and 260 mm, were used to calculate the normal daily growth of the population. The *t*-tests were used to compare the daily growth rate of the pugheaded fish with the average growth rate of normal fish in the population.

TABLE 2. Capture Dates and Total Lengths of a Pugheaded Brown Rockfish, *Sebastes auriculatus*, from Tiburon, California.

Capture date	*Total length (mm)*
10 December 1976	173
7 June 1977	198
2 December 1977	232
18 April 1978	240

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 3. Growth Periods and Daily Growth Rates for Pugheaded and Normal Brown Rockfish, *Sebastes auriculatus.*

Growth period number	*Date start*	*Date stop*	*Daily growth for pugheaded fish (mm)*	*Daily growth for normal fish (mm)*	*t-test value*	*Degrees of freedom*
1	10 Dec 1976	7 Jun 1977	0.1117	0.1927	−9.10*	20
2	10 Dec 1976	2 Dec 1977	0.1657	0.1495	1.55	4
3	10 Dec 1976	18 Apr 1978	0.1359	—	—	—
4	7 Jun 1977	2 Dec 1977	0.1932	0.1768	1.34	12
5	7 Jun 1977	18 Apr 1978	0.1342	0.1460	−1.28	6
6	2 Dec 1977	18 Apr 1978	0.0588	0.1517	−8.85*	32

* Significant at the 99% probability level.

The *t*-tests indicate that there were two periods (one and six) when the pugheaded fish's daily growth rates were significantly less than the average growth rates of the population (Table 3). The differential in growth between the pugheaded and normal fishes averaged −2.4, 0.5, and −2.8 mm per month during period 1 (December 1976 to June 1977), period 4 (June 1977 to December 1977), and period 6 (December 1977 to April 1978). Although the pugheaded individual grew more slowly than normal brown rockfish during the winter, its growth rate was the same during other times of the year.

The winter quarter (January, February, and March) is a period of limited food resources and stress for brown rockfish in San Francisco Bay, as demonstrated by major reductions in their fat reserves (unpublished data). The period of population stress and the period of growth reduction coincide, indicating that the pugheaded brown rockfish is not as efficient as normal fish when the population is under stress.

The possibility that pugheadedness reduces the ability of an individual to compete has been investigated for other species (Mansueti 1960, Leggett 1969). The growth rate of a pugheaded striped bass, *Morone saxatilis,* was compared to that of normal individuals by Mansueti (1960). He found the pugheaded individual to be relatively fit, but smaller than its normal counterparts at each age group. A similar comparison was made of a pugheaded Atlantic salmon, *Salmo salar,* by Leggett (1969) who found little indication (only a reduced length-weight ratio) that the pugheaded individual was unable to compete with normal fish in its population. Both of these studies and our data suggest that while a pugheaded fish may be relatively fit, pugheadedness limits the fish's growth. The reduced growth rate of the pugheaded brown rockfish and the timing of the reduction of fat reserves in the population suggests to us that the fish is relatively fit during periods of food abundance, but during periods of population stress and increased intraspecific competition, the pugheaded fish's fitness is lowered probably through reduced feeding efficiency.

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MOVEMENT AND SPEED OF DOLPHIN SCHOOLS RESPONDING TO AN APPROACHING SHIP

D. AU AND W. PERRYMAN[1]

ABSTRACT

Eight dolphin schools of the species *Stenella attenuata*, *S. longirostris*, and *S. coeruleoalba* were approached by ship and observed from a helicopter in the eastern Pacific to study their response to the vessel. All schools swam away from the projected track of the aproaching ship. Their movement, relative to the ship, followed paths that curved around the ship. Average swimming speeds while avoiding the ship varied from 5.1 to 8.8 knots. In some cases avoidance apparently began at 6 or more miles away from the ship. The effect of this behavior on shipboard censusing of dolphins is discussed.

In the eastern tropical Pacific, tuna fishermen encircle with purse seine nets schools of certain small cetaceans, mainly spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris*, to capture the yellowfin tuna, *Thunnus albacares*, with which they are associated (Perrin 1969, 1970). The resulting incidental kill of dolphins has led the National Marine Fisheries Service to study the status of these cetacean populations, as required by the Marine Mammal Protection Act of 1972. Data collected from commercial fishing boats and research vessels are important in determining the distribution and abundance of the dolphins.

In the areas of intensive "porpoise fishing," dolphins are apparently learning from their experience with nets and fishing vessels. The animals are recaptured with purse seines frequently enough to have possibly learned to position themselves within the net to better facilitate their own release (Pryor and Kang[2]). More importantly, they may also have developed various behaviors to avoid detection by a fishing vessel and to reduce their chances of capture (Pryor and Kang footnote 2; Stuntz and Perrin[3]). Dolphin schools, especially of the spotted and spinner dolphin species, commonly swim rapidly away from approaching ships. This behavior is our usual observation when studying dolphins from research ships.

In November 1976 we conducted a study to describe ship-avoidance behavior of dolphins. The purpose was to quantitatively describe school trajectories around an approaching ship and to evaluate the effect on shipboard censusing of dolphins. This study also allowed us to measure the swimming speeds of the schools and to make observations on school structure and behavior.

METHODS AND MATERIALS

We conducted this study from the NOAA Ship *Surveyor*, a 300-ft (91.4 m) steam-powered research vessel, and its Bell[4] 204 helicopter. We worked in the study area, the vicinity of Clipperton Island (lat. 10°15′N, long. 109°10′W) in the eastern Pacific, for 9 d (26 November to 4 December 1976). During six of these days, we made observations from the helicopter, flying twice daily in a crossing pattern ahead of the ship's track (Fig. 1). This enabled us to detect dolphin schools ahead of the ship and to follow the sequence of events leading to avoidance or the detection of the school by the shipboard observers. The 2.5-h flights began in midmorning (ca. 0900 h) and early afternoon (ca. 1330 h) to take advantage of the best lighting conditions for aerial observations and photography. Air speed was about 80 kn (1 kn = 1.85 km/h) at altitudes between 1200 and 1800 ft (366-

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

[2] Pryor, K., and I. Kang. 1980. Social behavior and school structure in pelagic porpoises (*Stenella attenuata* and *S. longirostris*) during purse seining for tuna. Southwest Fish. Cent. Admin. Rep. LJ-80-11C.

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[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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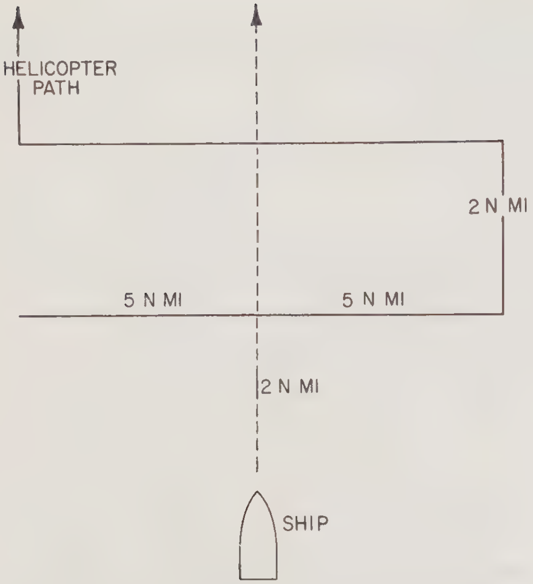

FIGURE 1.—Path of helicopter in front of ship during search phase of study.

549 m). Maximum altitude was determined by the cloud ceiling. During each flight, two scientific observers aboard the ship searched independently with 20 × 120 mm binoculars for dolphins. The observers were not in communication with the helicopter and were generally unaware of its position because of its range and because of their visual concentration on the sea surface. The ship's speed was between 11 and 13 kn.

Once a school was located, the helicopter remained near the school to serve as a radar target to fix the position of the dolphins relative to the vessel. Each time the helicopter passed over the school, we signaled the deck officer aboard ship via radio to record our radar range and bearing. These measurements from the ship were taken at successive time intervals to enable tracking the movement of the school. There was no indication to us that the helicopter affected school behavior. Indeed, the schools usually appeared to be swimming calmly throughout the tracking, until the ship approached to within a mile of the dolphins. During this tracking phase, ship course changes were minimized in order to determine how closely the school would pass the approaching vessel if not pursued. In some cases the ship was turned so its projected track would pass near the school, but course changes were minimal thereafter.

The shipboard radar used was a Decca-RM 1630. Its rated accuracy is to within 300 yd (274 m) of range at a distance of 10 nmi (18.5 km) and to within 1° of angular bearing. The radar measurements were made by a trained deck officer.

At the end of the tracking phase the ship approached closely or followed each school until the observers aboard had completed their estimates of school size and species composition. Meanwhile, we continued to take aerial photographs (35 and 70 mm still and 16 mm movie) and notes on school size and behavior that had begun when the school was first sighted. The movements and speeds of the schools as described below do not refer to this last phase of the operation.

School movement and speed were calculated whenever possible from relative motion plots since such plots portray the situation as seen from a ship. Required information for each plot includes the time interval between radar fixes, the course and speed vector of the ship, and the relative motion vector of the school, as determined by the radar ranges and bearings (the method is described by Bowditch 1966). These data were then used to construct vector triangles which were solved to get school speed vectors. Distance (range) was measured in nautical miles (nmi) and speed in knots (kn). The results were checked by plotting the sequential, absolute positions of the vessel and school from the data on vessel speed and data on range and bearing of ship to helicopter (school). School movement was measured from this absolute plot, and speed determined from the time interval between fixes to give results that should be the same as those obtained from the relative motion plots. When the ship made a course change, disrupting the relative position analysis for that time interval, the absolute position plot was the only solution.

A hypothetical example of a relative motion plot is presented in Figure 2. The ship is at the center (0) of the polar plot, proceeding straight ahead (000° or top of plot). Sequential radar ranges and bearings, from the moving ship to a dolphin school, are obtained at 0800, 0815, ..., and 0900 h. These fixes are plotted, and the line connecting them shows the relative motion of the school that is passing around to the right of the ship. The actual swimming vectors of the school, which produce this relative motion, can be obtained by solving vector triangles such as that shown at the center of the plot. For example, the

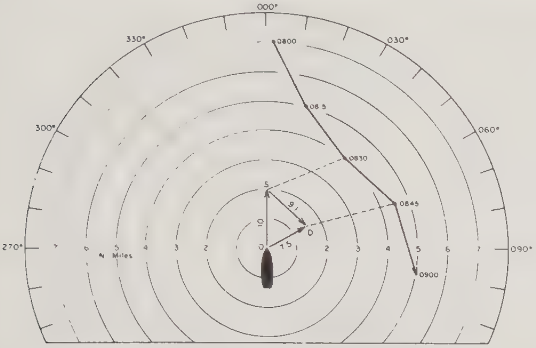

FIGURE 2.—Example of relative motion plot and calculation of school swimming vector.

relative motion between 0830 and 0845 h is equivalent to a relative velocity vector of 9.1 kn heading 134°. Projecting this vector (SD) onto the ship's vector (OS), which is 10 kn heading 000°, the school's swimming vector (OD) is obtained by vector subtraction as shown. In this case the swimming vector is 7.5 kn, heading 060°, and is the average swimming velocity between 0830 and 0845 h. Notice that the relative motion line is defined by ranges and bearings while the triangle at the center is composed of speed vectors, where, for convenience, 10 kn is defined as having magnitude 0 to 2 on the mile scale.

RESULTS

Vessel Avoidance

We were able to follow eight dolphin schools with the ship and helicopter (Table 1). The species were the spotted dolphin, the spinner dolphin, and the striped dolphin, *S. coeruleoalba*. All eight schools continuously adjusted their

TABLE 1.—Summary of dolphin schools observed from helicopter.

School	Species	Date and position	Local time (h)	Initial		School[1] size	Behavior relative to distance from ship[2]
				Range (nmi)	Speed (kn)		
1	*Stenella attenuata* + *Stenella longirostris*	11-26-76 (11°54′N 107°13′W)	0950	5.6	5.8	100	At 3.5 mi ship changes course and school increases speed to 8.3 kn. Between 1.9 and 2.6 mi school veers 40° to right across ship's path; as ship's path is crossed, school alters course again to head directly ahead of ship. At 2 mi school is in 2 groups running very purposefully with little intraschool deviations. Cruising smoothly at 5-6 kn with little splashing during most of vessel approach; strong evasive maneuvers at 100 m by group closest to ship. Two species incompletely mixed; many adults and juveniles in school.
2	*Stenella coeruleoalba*	11-27-76 (8°27′N 107°07′W)	0938	6.2	4.3	50	School initially "porpoising" gently as a loose aggregation, moving away to ship's right. At ca. 6.0 mi ship changes course; school veers 108° to left, accelerating to 5.8 kn. At ca. 5.0 mi school turns left again, still moving away at ca. 5.5 kn. At ca. 3.3 mi ship changes course and school accelerates to 6.3 kn temporarily. Between 2.0 and 3.0 mi school turns more to left; still running smoothly at 5.5 kn with little splashing. As ship passes 2.0 mi to right of school, it veers sharply left, continuing on almost opposite course as ship. Individuals bunching up at 1.8 mi. At times school composed of 4 groups. At 1.5 mi school speed is 8.3 kn. At 0.9 mi school running smoothly ahead of ship; a portion breaks off to right at ca. 100 m distance.
3	*Stenella attenuata*	12-1-76 (10°00′N 108°01′W)	0935	5.2	6.4	15	School initially seen under ca. 100 feeding boobies (*Sula* sp.), moving away from ship. At ca. 4.3 mi school accelerates to 7.8 kn then slows to 6.2 kn. At 3.5 mi school turning to right. Between 2.0 and 3.0 mi school swimming smoothly at ca. 5.0 kn; birds flying, rafting, or diving; most working ahead of school; later they form 2 large rafts behind school. By 1.5 mi school speed has increased to 7.2 kn. As school passes to left of ship at ca. 1.5 mi, it accelerates to 13 kn and veers to left. Birds have ceased feeding inside of 2 mi distance. School begins strong evasive maneuver at ca. 1/4 mi distance.
4	*Stenella attenuata*	12-2-76 (9°30′N 109°39′W)	0823	6.2	3.8	350	Initially detected as bird target by radar. Between 4.2 and 4.9 mi school changes course sharply away from ship, increasing speed to 4.6 kn, then slowing to 2.9 kn. At 3.0 mi much splashing in running school; some long, flat leaps seen. School becoming more scattered. Birds toward rear of school; later are scattered over school. At ca. 3.2 mi ship makes 90° turn to left; school veers 94° to left and increases speed; much running leaps seen; by 3.0 mi school speed is 6.5 kn. Between 2.5 and 3.0 mi main group in school turns toward ship; moments later they reverse their course again.

directions of swimming, by small increments, so that the distance between the school and the ship's projected track tended to increase continuously with time. The schools were either already proceeding on courses directed away from the ship when first sighted or made sharp course changes away from the vessel soon after. Several schools were moving off at relatively high speed when first seen. All the schools were evidently avoiding the ship. The behavior that indicated avoidance is summarized in Table 2 for each school. It appeared that avoidance behavior sometimes had begun when the school was still 6 or more nautical miles away from the ship.

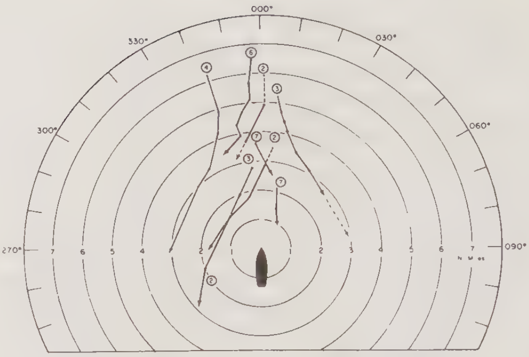

FIGURE 3.—Relative movement plots of five schools (nos. 2, 3, 4, 6, 7), showing the apparent motion as seen by a shipboard observer. Dotted lines are by dead reckoning.

Sufficient positioning data were collected from six of these schools to prepare diagrams of their movement relative to the approaching ship (Figs. 3, 4). The first school, school 1, is not plotted because frequent course changes by the ship during its tracking made relative movement difficult to portray. The path of relative movement of any of these schools, drawn by connecting the sequential series of radar fixes of the school as the ship moved forward, does not

TABLE 1.—*continued.*

School	Species	Date and position	Local time (h)	Initial Range (nmi)	Initial Speed (kn)	School[1] size	Behavior relative to distance from ship[2]
							At 2.5 mi individuals begin to bunch up; school in form of large arc with some scattered animals on the sides; birds no longer feeding. At 1.6 mi school is again scattered. Within 0.5 mi parts of school breaking away from ship's path; birds rafting nearby.
5	*Stenella attenuata* + *Stenella longirostris*	12-2-76 (9°39′N 109°48′W)	0953	5.8	ca. 2.6	300	Initially seen with many birds ahead and to right of school. School speed is ca. 2.6 kn. At 3.3 mi school changes course sharply away from ship and speed accelerates. Animals running with compact ranks at rear of school; few birds over school now. At 3.0 mi school running smoothly at ca. 8.4 kn. At 2.2 mi individuals appear confused, going in various directions within oval shaped school. At 2.0 mi a group temporarily heads toward ship before reversing course; school speed is 9.3 kn. At 0.6 mi many circuitous movements seen among small subgroups. School passes to ship's left; all individuals uniformly running from ship at 8-9 kn; birds rafting ahead. Ship turns toward school at ca. 0.5 mi; school splits ahead of ship at ca. 200 m; each dolphin species goes to different side of ship.
6	*Stenella attenuata*	12-3-76 ca. (9°31′N 110°30′W)	1032	6.9	ca. 10.0	40	School initially seen as running, oval mass moving off at ca. 10.0 kn with much splashing. At 6.5 mi school is in 2 groups moving smoothly in arc with little splashing. At 5.7 mi school is in 2 groups moving smoothly at 8.5 kn. At 5.1 mi school is composed of a dense and a scattered section; many direction changes among subgroups. School speed is down to 7.0 kn. At 4.5 mi school is scattered; composed of 3 large groups; many direction changes seen; speed is ca. 9.0 kn again. Between 3.5 and 4.0 mi school speed decreases to 7.6 kn then increases to 9.3 kn as school begins passing to ship's left.
7	*Stenella attenuata* + *Stenella longirostris*	12-3-76 (10°00′N 110°30′W)	1440	3.6	8.8	150	Initially swimming smoothly at ca. 8.8 kn with little splashing; scattered individuals at rear of school. At ca. 3.0 mi school still holding similar course with speed of ca. 7.0 kn; 50-70 birds over school. At 2.4 mi ship changes course and school also changes course and increases speed; birds scattered over the scattered school. At 1.4 mi school running smoothly in loose groups, going ca. 6.0 kn. At <1.0 mi smoothly running school is scattered by ship.
8	*Stenella coeruleoalba*	12-2-76 (10°27′N 110°01′W)	1420	0.9	—	65	A leaping, loosely aggregated school at 0.9 mi. At 0.7 mi school running with increasing speed as ship turns toward school. At 1/4 mi school forming an arc ahead of ship.

[1] Estimated from aircraft.
[2] Distances and behavior from radar ranging and bearing, interpolation of movement trajectories, and field notes. Distances in nautical miles.

TABLE 2.—Range and behavior when vessel avoidance was first seen.

School number	Species	Range (nmi)	Behavioral indication of vessel avoidance
1	*S. attenuata* *S. longirostris*	5.6	School rapidly swimming away from ship at 5.8 kn when first sighted from helicopter.
2	*S. coeruleoalba*	ca. 6.0	As ship turned toward this school, the animals accelerated from 4.3 to 5.8 kn and turned away from the ship.
3	*S. attenuata*	5.2	School rapidly swimming away from ship at 6.4 kn when first sighted from helicopter.
4	*S. attenuata*	ca. 4.6	School made sharp course change away from ship and accelerated to 4.6 kn.
5	*S. attenuata* *S. longirostris*	3.3	School turned away from ship and accelerated from 2.6 to 8.4 kn.
6	*S. attenuata*	6.9	School moving away from ship at high speed (ca. 10 kn) when first sighted from helicopter.
7	*S. attenuata* *S. longirostris*	3.6	School moving away from ship at high speed (8.8 kn) when first sighted from helicopter.
8	*S. coeruleoalba*	0.9	School leaping away from ship when first sighted from helicopter.

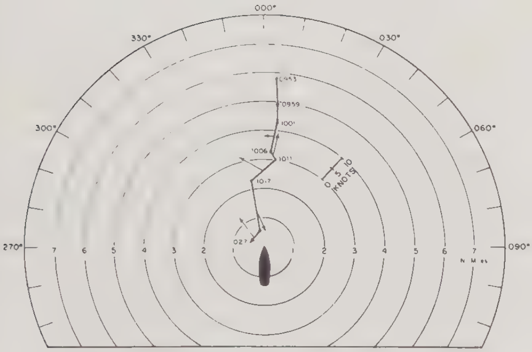

FIGURE 4.—Relative motion plot of school 5, showing its apparent motion as seen by a shipboard observer. Small arrows show actual school velocities at various distances. Note heading reversal shown at 1.5 mi.

represent the actual swimming directions of the school, but rather the resultant of the swimming velocity of the school and the movement of the vessel. The ship's position remains at the center of each diagram, and swimming direction is depicted relative to the ship's heading, which is toward the top of the page. The plots therefore show the apparent motion of the schools as seen by an observer aboard the ship. A break in the relative motion line for a school represents a course change by the ship.

The relative movement of five schools (schools 2, 3, 4, 6, and 7) are depicted in Figure 3 where, for clarity, swimming speed vectors and the times of radar fixes are not included. It is important to realize however, that along each relative motion line the school is generally swimming away from the oncoming ship. We have extrapolated parts of the movements of schools 2 and 3, based upon our observations of their activity. The movement of each of the five schools is depicted as though moving relative to the same ship heading (000°). These schools are described in two groups.

The first group (schools 2, 3, 4, and 6 in Figure 3) was initially located between 5 and 7 nmi from the ship. After some initial adjustments in heading, the schools' swimming directions remained relatively constant. The resultant paths of the dolphin schools thus veered from the track line at a nearly constant angle after this initial period. Assuming that the schools would remain approximately on the same course and extending their lines of relative movement, it appeared that these schools would have passed no closer than 2.4 nmi from the ship, had it remained on the same course. School 4 exhibited additional notable behavior that is not shown in Figure 3. When the school had passed abeam, the ship was turned towards the school. Five minutes later, at a range of about 2.5 nmi, a large section of the school turned and headed toward the ship in a tightly aggregated group. Within a minute this section reversed course again and rejoined the original school.

The second group (schools 2, 3, and 7 in Figure 3) consists of schools that were between 2.6 and 3.7 nmi away, either when first sighted (school 7) or after the ship had turned toward the school at the end of an initial tracking period (schools 2 and 3). The lower and separated segments of the latter schools' tracks represent the relative movements after the ship had turned. These schools were then within 0.4 nmi of the ship's projected track. Even so schools 2 and 3 subsequently came no closer than 1.4 nmi to the ship. School 7, by its initial projected trajectory, would have come no closer than 1.5 nmi, but after the ship turned toward it, its new resultant path would have taken it about 0.7 nmi from the ship.

School 5 behaved quite differently from the others. Both relative movement, time of radar fixes, and swimming speed vectors are shown for this school (Fig. 4). The swimming speed vectors, shown as arrows attached to the relative motion line between various time and distance intervals, are drawn proportional to the calculated swimming speeds (Table 3).

School 5 was probably feeding when the bird flock associated with it was first detected on the ship's radar at a distance of 5.8 nmi. The distance and bearing plots of the birds indicated erratic movement. Later, in the tracking-by-helicopter phase, the first two ranges and bearings showed the school moving at only 2.6 kn. The inferred feeding behavior from this is consistent with the feeding behavior described by Norris et al. (1978), as well as other observations by us in the eastern Pacific. At a closer range of about 3.3 nmi from the ship, the school's behavior changed radically as it altered course by 97° to the right and increased its speed to 8.4 kn, turning on a course that would have taken it 2.0-2.5 nmi abeam of the passing ship. Between 2.3 and 3.0 nmi the school again shifted course, this time by 70° to the left, and increased its speed to 9.4 kn. When this school reached a point about 0.5 nmi from the track line and 2.3 nmi from the ship, its behavior changed again. Individuals and subgroups within the school began swimming in many different directions, making large changes in course heading. Suddenly the main body of the school turned nearly 180° and swam toward the ship at high speed (~9 kn). After closing to within 1 nmi of the ship, the school reversed itself again, and thereafter swam rapidly away from the vessel. This type of "error" in choice of avoidance heading was only seen in schools 4 and 5, which were both relatively large schools (300-350 individuals estimated).

School Speed

While avoiding the ship, the speeds of the first seven schools varied between 2.5 and 13.1 kn, with average speeds between 5.1 and 8.8 kn (Table 3). The eighth school was too close to the ship for ranging measurements by radar. There was no apparent difference in swimming speeds among the three species observed. Substantial variation in speed occurred in all seven schools. Schools 1, 2, 3, and 4 swam at speeds that averaged between 5 and 7 kn. Schools 6 and 7 had the

TABLE 3.—School swimming speed vectors.

School	Time (h)	Range[1] (nmi)	Bearing[1]	Course[2]	Speed[2] (kn)
1	0950	5.6	088°		
	1015	3.6	105	128.2°	5.8
	1022	3.3	107	128.6	8.3
	1030	2.6	104	126.3	5.7
	1035	1.9	112	166.7	5.3
	1042	1.4	115	114.5	6.2
	1049	0.8	110	100.0	6.8
	1101	0.7	310	092.0	4.0
					[3] $\bar{x}=6.0$
2	0938	6.2	016		
	0942	5.9	026	118.3	4.3
	0952	4.9	026	010.6	5.8
	1000	3.7	017	330.7	5.5
	1006	2.9	008	324.6	6.3
	1013	1.8	352	304.6	5.5
	1019	1.5	320	315.2	8.3
	1028	2.0	255	285.2	5.7
	1033	3.0	230	216.5	5.6
	1045	2.5	212	223.6	6.0
	1051	2.0	200	229.0	5.9
	1104	0.9	179	182.8	6.3
					$\bar{x}=5.9$
3	0935	5.2	295		
	0940	4.7	297	300.9	6.4
	0943	4.4	299	308.9	6.5
	0947	4.1	301	298.8	7.8
	0953	3.5	308	316.6	6.2
	0959	3.1	320	326.2	7.8
	1006	2.8	340	335.1	6.2
	1016	2.9	019	354.2	5.0
	1023	2.0	010	337.0	[4] 4.9 (1017-1023)
	1029	1.6	353	005.0	6.6
	1032	1.5	335	334.5	7.2
	1035	1.8	296	264.0	13.1
					$\bar{x}=7.1$
4	0823	6.2	333		
	0829	4.9	333	086.5	3.8
	0835	4.2	330	349.5	4.6
	0841	3.2	318	261.9	2.9
	0845	3.0	305	282.5	6.5
	0857	3.2	256	263.2	5.2
	0915	1.6	255	265.8	6.2
					[4] $\bar{x}=5.1$ (0835-0915)
5	[5] 1001	4.3	356		
	1006	3.3	354	264.2	2.6
	1011	3.0	357	001.2	8.4
	1017	2.3	339	290.8	9.4
	1022	0.6	334	148.4	9.3
	1027	0.5	268	314.7	7.9
					[4] $\bar{x}=8.8$ (1011-1027)
6	1032	6.9	281		
	1038	6.5	278	273.6	10.0
	1050	5.7	277	279.2	8.5
	1056	5.1	277	284.4	7.0
	1102	4.7	273	262.0	9.2
	1108	4.3	270	270.1	8.8
	1112	3.9	271	297.4	7.6
	1121	3.4	258	253.3	9.3
					$x=8.6$
7	1440	3.6	167		
	1446	3.2	170	182.4	8.8
	1452	2.6	177	199.1	6.6
	1458	2.1	191	215.3	7.5
	1505	1.4	197	175.6	6.0
	1508	1.0	205	164.6	2.5
	1519	1.1	240	242.0	11.5
					$\bar{x}=7.2$

---

[1] Range and bearing of school from ship at times appropriate to the speed calculation. If notable, behavior at these and other times are reported in Table 1.

[2] Speed vectors pertain to time intervals ending at times listed unless otherwise indicated. Calculations are from relative or absolute plots involving ship motion.

[3] Mean school speed refers to times when school is responding to ship.

[4] Time interval for this calculation.

[5] This school was actually sighted at 0953, but measurements did not begin until 1001.

highest initial speeds, 10.0 and 8.8 kn, respectively, and had average speeds of 8.6 and 7.2 kn, respectively. Both were moving with the waves in a Beaufort 4 sea state (11-16 kn wind) and were probably utilizing the forward momentum of the swell as described by Lang (1975). The speed of school 5 was also high (>8 kn) after the first 5 min that it was observed. Its average speed while actively avoiding the ship was 8.8 kn. This higher sustained speed may have been related to its level of excitement that was evident in its apparently confused state, when it turned toward and then away from the ship (Table 1, Fig. 4). Schools 3 through 7 showed some tendency for increased speeds as the ship drew nearer.

Swimming Behavior and School Structure

Field descriptions of each school, and later study of the aerial movie and still photographs, revealed no obvious indication of dominant, or leading, individuals or subgroups. The schools were seen to progress in an almost amoeboid fashion with subgroups of two to five individuals striking off in different directions or accelerating to higher speeds, then drifting back to the main body of the school if not followed by others in the school. Although individuals and subgroups within a school were constantly changing course, sometimes abruptly, the heading of the main body of the school remained nearly constant or changed slowly. The schools appeared as loose aggregations of individuals and small subgroups, most proceeding along similar headings. Individualistic rather than coordinated movements were the general feature of these schools. The schools appeared to be one-layered, i.e., groups of animals were not swimming beneath others.

As the vessel closed to within 2 nmi of the schools, the subgroups within the schools were seen to be increasingly oriented in lines abreast. Animals in the rear third of a school could be seen swimming faster than those ahead. The result was that the width of a school in the direction of its swimming axis narrowed as the distance between ship and school decreased.

DISCUSSION

Our first impression from the observed school behavior and structure was that the dolphins were not noticeably disturbed by the vessel's presence. Only at a distance of less than a mile did bunching or compaction of the relatively dispersed individuals and small subgroups become common and did the schools obviously appear to be running, i.e., in flight (Table 1). Radical, evasive maneuvers were not regularly seen until the last 200 m of distance between ship and school. Examination of the relative motion plots and the consecutive vectors of swimming speed and course made it clear, however, that the dolphins were actually avoiding the ship much earlier, sometimes beginning at distances approaching the horizon for a shipboard observer. Though ship-avoidance behavior should not be surprising, considering the extent of "porpoise fishing," in the study area, it is a behavior not easily studied from a surface platform. These observations have important implications relative to population studies of dolphins, especially those conducted from ships.

Because a shipboard observer sees a dolphin school increasingly in profile view as distance increases, an understanding of its structure and behavior is helpful for proper interpretation of its characteristics. A travelling school appears to be a loose aggregation of relatively widely separated individuals or subgroups of 2-5 animals. Rather than being made up of relatively few, tight subgroups of various sizes, as observed for spotted dolphins in a purse seine (Norris et al. 1978), most of the animals in these schools appeared to be swimming independently, as individuals or in pairs. This school configuration appeared typical all during vessel avoidance, except at radial distances of less than a mile from the ship.

The schools we observed remained inconspicuous to the shipboard observers because they swam smoothly, without much splashing, at speeds that averaged 6.8 kn. Even at swimming speeds of 7-9 kn, the animals often broke the water surface with little commotion and swam most of the distance between breaths just under the surface. Bursts of higher speed, with attendant long leaps (2-3 body lengths) and large splashes, occurred only temporarily.

The swimming speeds presented in Table 3 pertain to these pelagic dolphins when swimming in the cruising mode, i.e., moving smoothly with little splashing for sustained periods. The higher observed speeds of 7-9 kn are still in the upper range for prolonged cruising speeds of smaller dolphins (Webb 1975). That this must be so is indicated by the fact that research ships moving at 10 kn can always closely approach these dolphins, provided that the schools can be followed. Evidently school speeds greater than that of the ship can be maintained only temporarily. Dolphins that do break into the "running," or leaping swimming mode, must be exceeding a certain "crossover speed." This is the swimming speed above which a leaping locomotion becomes more efficient. It is calculated to be somewhat in excess of 10 kn (Au and Weihs 1980). Thus several lines of evidence indicate that cruising speeds are <10 kn, as we in fact measured. Dolphins of course are capable of temporary higher speeds than reported here. Top burst speeds as high as 14.5 kn have been measured for *Tursiops truncatus* (Lang and Norris 1966) and 21.4 kn for *S. attenuata* (Lang and Pryor 1966).

Because the faster, leaping locomotion produces much splashing, dolphins that avoid ships by moving away more slowly at cruising speed obviously are more difficult to detect from the ships. The initial avoidance probably proceeds at cruising speed because the dolphins are not yet highly alarmed at the distances at which detection of the ship and evasion begins.

The evasive behavior of dolphins perhaps has its most important implication relative to school density studies conducted from ships. In particular the line-transect method (Seber 1973; Burnham and Anderson 1976), which can be employed for absolute density estimation of schools, may be affected. An important requirement of the method is that the schools do not move, or move randomly or little, relative to the speed of the observer. However, schools are evidently capable of avoidance movements at speeds approaching that of the ship. Therefore positions of schools relative to the ship and prior to movement that are required to describe the probability of sighting a school cannot be obtained if there is movement. Only if the school trajectories were known could the observed positions be corrected. The probability of sighting is usually obtained from the distribution of perpendicular distances that are a transformation of the relative positions of sighted schools. Laake (1978) and Burnham et al. (1980) emphasized that when school movement occurs, both the probability functions describing detectability and the altered animal distribution are completely confounded in the distribution of observed perpendicular distances. School movement also violates the critical assumption that all schools initially on the track line will be seen. Therefore, line transect methods for absolute density estimation usually cannot be used when avoidance movements occur.

It is easy, however, to understand how avoidance behavior reduces the probability of sighting a school from a ship. Without movement this probability would be (Burnham and Anderson 1976)

$$\frac{1}{w}\int_0^w g(x)dx$$

where w is the half width of the swath being searched, which could be the horizon distance, and $g(x)$, the detection function, is the probability of sighting a school that is initially at perpendicular distance x from the track line. The function, $g(x)$, is monotonically decreasing from 1 on the trackline ($g(0) = 1$). Therefore, schools avoiding a ship by effectively moving farther abeam must obtain a value to $g(x)$, say $g(x)^1$, that is less that that at its initial distance x. These reduced values, $g(x)^1$, replace the original values of $g(x)$ at all initial perpendicular distances where avoidance movements began. The area under this altered detection curve (i.e., the plot of $g(x)^1$ against x), which determines the new probability of sighting a school from the track, is accordingly reduced. Reasonable models of the detection function and how it is altered by avoidance behavior can be constructed to show that this reduction can be considerable.

If dolphins do obtain lower $g(x)$ values from their avoidance trajectories, the behavior would be advantageous. This seems entirely possible considering that the schools can cruise at speeds approaching that of many research ships (Table 3) and apparently can detect and continue to sense a ship from considerable distance. Evidence of the latter are the distances at which avoidance behavior was apparent (Table 2) and the near simultaneous changes in school course or speed following course changes by the ship. Such changes occurred at 3.5 mi in school 1, at 6.0 and 3.3 mi in school 2, at 3.2 mi in school 4, and at 2.4 mi in school 7 (Table 1).

With significant reduction in sighting probability possible from avoidance, it would be useful to empirically determine the actual probabilities, $g(x)^1$, or to model this behavior. We expect, however, that the specifics of avoidance trajectories as well as the probabilities would vary greatly with species, populations and their experience, and the specific behavioral activity of the school when encountered. The type of ship involved and environmental conditions may also affect avoidance behavior.

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PERSPECTIVES

Ocean Sciences in Relation to Living Resources

ANDREW BAKUN

Pacific Environmental Group, Southwest Fisheries Center, NOAA, Monterey, CA 93940, USA

JAN BEYER

Danish Institute for Fisheries and Marine Research, Charlottenlund, Denmark

DANIEL PAULY

International Center for Living Aquatic Resource Management, Manila, Philippines

JOHN G. POPE

Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Lowestoft, England

AND GARY D. SHARP

Food and Agriculture Organization, Fisheries Department, Rome, Italy

BAKUN, A., J. BEYER, D. PAULY, J. G. POPE, AND G. D. SHARP. 1982. Ocean sciences in relation to living resources. Can. J. Fish. Aquat. Sci. 39: 1059 – 1070.

The Intergovernmental Oceanographic Commission's Resolution XI-17 on Ocean Sciences in Support of Living Resources specifies that programs should be formulated in applied ocean research related to fishery problems. In this report we identify some types of needed research. We discuss the relative importance of the various life history stages to the question of resource variation regarding difficulties in sampling or studying on relevant scales. Our report stresses identification and accounting for causal climate-driven ambient variations. Some testable hypotheses relating the larval stages are given as examples of useful research. We also describe research needed on predation and species interactions. Examples of specific systems where important ecological processes need intense study are given. Upwelling areas, coral reefs, tropical and shelf demersal fisheries, and the open ocean fisheries each require different types and scales of study. The importance of data accessability and multidisciplinary research activities, beginning with dialogues between the ocean research and fishery resource scientists is paramount to successful completion of these tasks. The examples provided may stimulate further effort to identify resource research problems and programs for resolving them.

Key words: ocean science, living resources, life history cycles, fishery recruitment, predation, species interactions, fish eggs and larvae, vertical stability of the ocean, advection, convergence and divergence, upwelling systems, coral reefs, tropical demersal fisheries

BAKUN, A., J. BEYER, D. PAULY, J. G. POPE, AND G. D. SHARP. 1982. Ocean sciences in relation to living resources. Can. J. Fish. Aquat. Sci. 39: 1059 – 1070.

La résolution XI-17 de la Commission intergouvernementale d'océanographie concernant les sciences océaniques à l'appui des ressources vivantes spécifie qu'il faudrait formuler des programmes de recherche océanologique appliquée axés sur les problèmes de la pêche. Le présent rapport identifie quelques genres de recherches nécessaires. On traite de l'importance relative des diverses étapes du cycle évolutif dans la variation de la ressource, en ce qui a trait aux difficultés d'échantillonnage ou d'étude sur une échelle appropriée. Le rapport met l'accent sur l'identification et l'explication des variations ambiantes causales qu'entraîne

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le climat. Quelques hypothèses vérifiables établissant un rapport entre les stades larvaires sont donnés comme exemples de recherche utile. On décrit aussi la recherche nécessaire sur la prédation et l'interaction des espèces, et on donne des exemples de systèmes spécifiques nécessitant une étude intense des principaux processus écologiques. Les zones de remontée d'eau profonde, les récifs de coraux, les pêches démersales dans les tropiques et sur la plate-forme continentale, et les pêches en haute mer nécessitent des recherches de types et d'échelles différents. La facilité d'accès des données et des activités de recherche multidisciplinaire, débutant par des dialogues entre les scientifiques en recherche océanique et les scientifiques en ressources halieutiques, sont d'une extrême importance pour l'achèvement de ces tâches. Les exemples fournis peuvent stimuler des efforts supplémentaires pour identifier les problèmes de recherche sur les ressources et les programmes pour résoudre ceux-ci.

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Background to the Report

At its 11th Assembly the Intergovernmental Oceanographic Commission (IOC) passed Resolution XI-17 on Ocean Sciences in Support of Living Resources (OSLR). The purpose of this resolution was to promote development of plans for major oceanographic studies of the physical–ecological interactions of importance to fishery resource-related problems for submission to the 12th Assembly in 1982. IOC and the Food and Agriculture Organization (FAO) appointed two rapporteurs, Dr T. Austin and Dr J. A. Gulland, respectively. In consultation with the IOC Secretariat, they decided that the most useful approach was to convene a small group of individuals actively involved in research on multispecies and climate–environment physical processes applied to fisheries problems, which could provide a useful survey of present-day thinking on how to begin formulating such plans. This document, originally identified as the Report of the "Group of Four," was circulated widely throughout the oceanographic community as a stimulus for comments and a basis for thoughtful progress toward the objectives of the OSLR resolution.

The fact that both distributions and abundances of resource species are related directly to environmental properties such as temperature, food, and oxygen is of primary importance. However, few well-defined examples are available of direct causal relationships between variations in abundance and environmental processes beyond the seasonal "displacement" of the above properties or observations of nonusual events relative to some geographic base (i.e. North Atlantic cooling trend and cod occurrence).

Much of our ignorance in this regard can, I believe, be attributed to wrong-scale thinking. For example, studies of recruitment of fishes often integrate the entire early life history of these fishes into a single prerecruit class, and the relations between recruitment and subsequent production are sought from trying to match up only spawning biomass and recruits, with the residuals or deviations from any one of the numerous available stock–recruitment formulations being attributed to "environmental variations." The major proportion of the mortalities in most oviparous species occur in the prerecruit stages. The order of magnitude of the recruitment is therefore primarily dependent upon variations in about the 4th or 5th decimal place in these day-by-day, stage-by-stage probabilities of survival.

The single, most important distinction in the recently emerging approaches to these problems of recruitment is the idea that there are very important processes at scales relevant to survival of *individual* fish larvae and juveniles which must be encountered, or the larvae cannot survive. This implies that there are hierarchic hurdles to be faced resulting in variable and discontinuous mortalities rather than averages or constants.

Much of this current thinking is described for the problems of dealing with only first feeding of pelagic fish larvae in IOC Workshop Report No. 28 on the effects of environmental variation on the survival of larval fishes (1980). Increasing our knowledge of the trophic levels supporting this single stage and beyond will require intense multidisciplinary study.

The significance of environmental variability on the numerous trophic levels is the subject of many biological oceanographic studies. These often elusive intricacies of marine ecosystems are driven by solar energy which generates climatic events arising from diurnal, seasonal, and epocal processes of energy absorption, transfer, and dissipation, often months and thousands of kilometres away (i.e. El Niño) as well as daily, local events (i.e. insolation, wind, rainfall).

One major problem is our need to develop methods for measuring and monitoring directly or via proxies (i.e., upwelling or stratification indices) the directly causal processes important to the variations in survival of the numerous fishery resources. This means that appropriate scales need to be defined, that appropriate measurements be identified, and that sensors and equipment should be designed and employed to resolve these processes into useful signals.

Equally important is the training of fishery and oceanographic scientists in the principles and use of the sensors and equipment, long-term data collection, and the employment of cause-and-effect (or rational) hypothesis testing. This will certainly include experimental research in the laboratory as well as on the sea so as to provide evidence that there are true cause-and-effect linkages between the various important signals.

For example, without the fruitful, diligent research of many of the co-workers in Lasker's Laboratory, his hypothesis regarding the importance of small-scale phytoplankton stratification in the larval habitat to the survival of the California Anchovy (Lasker 1975) and other important pelagics might have remained speculative. However, the laboratory studies of Hunter (1972, 1976), Hunter and Thomas (1974), Arthur (1976, 1977), Lasker and Zweifel (1978), O'Connell (1976, 1980), O'Connell and Raymond (1970), and Methot and Kramer (1979) have provided supportive evidence for Lasker's hypothesis. They have also helped further define appropriate scales of sampling at sea and in the laboratory for improving our understanding of the conditions promoting survival of individual larval fishes in the sea.

From this same research group we have learned about rates of important egg and larval fish mortality processes due to cannibalism (Hunter and Kimbrell 1982), spawning site selection and predation (Alvariño 1980), and the significance of batch fecundity (Hunter and Goldberg 1980) to the interpretation of conventional egg and larval surveys.

In particular the California northern anchovy (*Engraulis mordax*) examples are stimulating, formative observations, employing new and classical methods yielding interactive research results from which we can begin to challenge the overintegrative "conventional wisdoms."

This extreme case of "focused" research could lead one to conclude that to investigate each important commercial species would require unlimited resources and expertize. In fact, this is not true. These examples provide numerous opportunities to test quickly or evaluate generalities of such fundamental processes as first feeding which must certainly be a common property of newly hatched fishes, onward through ecological and environmental properties which promote, or subsequently fix the limits of survival into the following stages or ecological challenges. Once a decision regarding causal processes has been reached, appropriate proxies can be identified and monitored on relevant scales.

These and many similar experiences have led to the formulation of this report.

As the experimental research activities in the world ocean become more restricted because of conflicts of interest and jurisdictional progress, it seems that both the applied and academic scientists will of necessity recognize their interdependence, even to the point of initiating required dialogues and mutual-objective research. The relative isolation which has been characteristic between marine science and fishing-related problems needs to be diminished. This has been said by so many for so long that it must be a real problem. OSLR is an opportunity for scientific collaboration, mutual dialogue and familiarization, and resolution of important worldwide problems. OSLR is both challenging and sobering. Perhaps OSLR will provide stimulus for the maturity of marine ecological research into the fruitful and valuable applied science it should become.

The Group met at FAO Headquarters, Rome, Italy (Fisheries Department), from October 14 to 17, 1980, and included the following persons: A. Bakun, J. Beyer, D. Pauly, and J. G. Pope (Chairman) as members of the 'Group of Four Scientists.' The two previously mentioned rapporteurs; G. Tomczak, IOC Secretariat; G. D. Sharp, FAO Fisheries Resource and Environment Division; H. Austin and FAO staff also took part in the discussions.

Obviously readers will recognize that so few people in so short a time could not address the problem in more general terms and still have something tangible for others to add to, or assault, as the case might be. Stimulation was the objective; problem definition and resolution is the product expected from the readers.

G. D. SHARP

The Report

Introduction

The Group decided to confine its discussions to ocean areas between 45°N and 45°S to focus attention on the fisheries problems of the developing world. This document was an attempt to identify gaps in our knowledge of important fisheries-related processes which might be closed, given the attentions of the ocean sciences, in the broadest sense. The Group saw many areas where research would be valuable. However, we noted that for this research to be useful in understanding fisheries problems, it would need to be conducted on a time-and-area scale appropriate to the fishery in question.

The Group agreed that oceanic research of all sorts was potentially valuable; however, for direct use, ocean research in support of resource science argues for close collaboration between fisheries and other ocean scientists at all stages of research.

Problems of fishery science arise from the need to answer questions posed by the fisheries management community, particularly in the face of the numerous conflicts of interests, i.e. among different methods of commercial fishing or commercial fishing vs. sport fishermen, or subsistence fishermen vs. public opinion, and, most important, restrictions imposed as conservation measures vs. exploitation interests. Some of these questions can be answered by the collection and interpretation of fisheries data (catch, effort, age structure data, etc.) but others have proved intractable on this basis. From experiences in well-studied areas such as the North Sea, California, and the waters around Japan, it is clear that problems of recruitment, availability, and species interactions cannot be solved from fisheries data alone.

Some conventional fishery-related questions generally asked and the problems posed are set out below:

Management tasks from the FAO perspective	*Empirical approaches and scientific problems*
1) For a region where fisheries are not fully exploited: identify the resource(s), describe their seasonal and long-term distribution patterns, and evaluate possible effects in neighboring fisheries.	Survey or exploratory fishing, comparison with data sets from known area, identify unconventional resources, identify efficient harvest methods.
(2) For a growing fishery: determine potential yield and its likely variability.	Identify population characteristics and population structure, estimate present abundance, investigate ecological interactions, compare natural and man-induced variations within and outside of area.
3) For both developing and developed fisheries: improve operating efficiency.	Locating fish stocks and their seasons and areas of vulnerability; investigate source of variance in vulnerability, including those that are due to environmental fluctuations; predict catches.
4) For a fully exploited fishery: set suitable constraints to achieve rational exploitation:	
a) For single species with uniform recruitment.	Estimate population parameters such as growth rate, onset of maturity, mortality rates at various stages.
b) For single species with variable recruitment.	Factors affecting recruitment, including minimum spawning biomass. Early estimation of year-classes.
c) For fisheries on several species.	Effects on one species of changing patterns of fishing on other species.

The problems relating to the first two questions are concerned with fisheries development. They are thus transitory problems which need coarse but timely advice. In many cases order of magnitude answers would be sufficient. Questions of operational efficiency and management, however, are permanent features of fisheries requiring more accurate advice which may be developed over a longer time frame. Operational questions may need to be answered to within a factor of 2 while management questions ultimately need to be understood with greater precision.

For these reasons the problems associated with questions of fisheries operations and management seem the most appropriate for the inputs of longer term scientific advice. The problems of (1) Availability (distribution, abundance, vulnerability to gears), (2) recruitment and life cycle or natural history variations, and (3) species interactions are the problems which seem most pressing in well-studied fisheries; however, this may not be the case for all systems. Therefore, the report considers questions arising from various stages of fish life cycles and also problems arising in the major ecological systems associated with the developing world. The proposed types of research at the locations suggested are in no way intended to be exhaustive. Rather they are in the nature of examples of what might be done.

Life History Cycle

DEFINITIONS OF LIFE HISTORY STAGES

The common denominator in the world major food fish resources is that oviparous fishes dominate the catches. Only a few exceptions are notable, i.e. *Sebastes* species, elasmobranchs, *Zoarces* species, etc. Therefore, in portraying a typical life cycle pattern it is appropriate to start with the egg in the water column and proceed by stages of development and characteristics of these stages toward the deposition of eggs in the subsequent generation. A simple circle diagram can be used to describe this pattern.

Stage I comprises entry of the egg into the environment (A), fertilization and subsequent prehatch larval development; hatching of the larvae (B) and subsequent development up through metamorphosis (C — loosely defined here as the time scales form or when dominant respiration switches to the gills).

Stage II includes the posttransformation developmental stages of juveniles (D) which precede entry of the fish into vulnerability to fishery operations (E). This is the least-understood stage in the life history cycle of many fish because there is no appropriate gear to sample them effectively during this stage.

Stage III includes the period from initial entry of the fish into the fishery or sampling operations (E), of juvenile to adult fishes before the onset of gamete maturation (F).

Stage IV is defined as that period from the onset of gamete differentiation and maturation (F) to the end of the reproductive period of the individual. This may be seasonal, annual, or continuing over varying time scales, depending upon the species. Also, egg maturation and subsequent spawning may happen once or several times in a lifetime, i.e. iterative within any year (Hunter and Goldberg 1981) or annual.

Life cycles determine susceptibility of the populations to short and longer term system variations, physical and/or ecological in nature. Early life history stages exhibit variations based on, for example, temperature or food conditions.

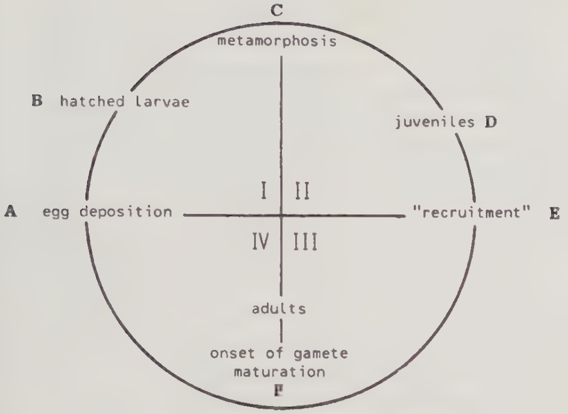

FIG. 1. A schematized life cycle of fishes.

"Ecological positions" shift continuously as fish grow, but these shifts are different, i.e. have differing rates of change, within and among species, and represent responses to system changes. Obviously death may occur at any point in the diagram.

A common starting point for oviparous species is the hatched larvae's need to encounter appropriate densities of appropriate foods to stimulate first feeding (from B on the diagram). The larvae that are *not placed* into the appropriate environment do not survive. Appropriate survival environments are 'windows' in time and space. They are probably not forecast by the adults in any direct sense in many coastal fishes. This is evidenced by their long or continuous spawning seasons. Other species having localized spawning (e.g. homing) and short reproductive seasons are tuned to relatively stable systems which are found to vary on the decade time scale as these populations also do (Iles and Sinclair 1982). More complicated reproduction behaviors are expected in the open ocean (oceanic) species because the patchiness and availabilities of species-specific "survival windows" may be on different and probably extensive time and area scales in the oceanic systems (Sharp 1981). These species must have a more definite ability to identify "appropriate larval survival habits" than the other species or there are more of these densely populated larval fish nurseries than is presently suspected.

The upper quadrants (I and II) of Fig. 1 represent stages in which survival is only rarely affected by man directly (except for pollution and habitat destruction). All stages are directly affected by environmental variations and this is the basis of several problems which could be tackled by scientific researchers.

Stage I — egg and larval survival — Extreme vulnerability and high rates of mortality characterize the egg and larval stage; this stage is considered the most critical to eventual recruitment. There are multiple interacting processes involved including feeding, growth, predation pressure, etc. at various substages. Because most of the available data are from the adult stage which is sampled by a fishery, it is a common practice to integrate the processes of Stage I, and of the juvenile stage (II) as well, by means of empirical stock—recruitment functions. Unfortunately these functions often provide poor fits to the observed data. The deviations are commonly attributed to environmental effects.

One way to view the problem is in terms of a multiple regression in which stock size (S) is included with environmental terms (E_i) as explanatory variables. For example, the formulation:

$$\log R/S = a_0 + a_1 S + a_2 E_1 + a_3 E_2 + \ldots$$

is a Ricker (1975) function modified by environmental terms.

Obviously, if the dependence on S is less important than the environmental dependence, neglecting environmental terms leads to a poor estimate of the dependence on S (which is the only term that can be influenced by management). However, there is always an extremely limited number of data points available. Thus, the number of explanatory variables must be reduced to a minimum. This should be done on rational grounds, based on the best available understanding of cause—effect relationships between recruitment and environmental factors. Terms relating to multispecies interaction (for example, the size of a predator stock) might be incorporated similarly.

Such a procedure is an example of the combination of the rational (cause—effect) approach, which is based on understanding of the physical and biological processes involved, and of the empirical approach in which the functional relationships are defined by analysis (e.g. by regression) of available data. A strictly rational approach is usually not feasible. The complex linkages between environmental processes and biological consequences are extremely difficult to observe or to investigate experimentally; the quantitative information needed to construct rational models of those linkages is most often unavailable. On the other hand, the empirical approach is hampered by a lack of sufficient data points. Fishery data characteristically yield one estimate of stock size and recruitment per year; the available time series rarely exceed several decades and most often are of the order of 10—20 yr. To sort out a multitude of possible environmental effects by statistical means from a series of 10—20 data points is not possible. Moreover, the time series often contain significant autocorrelation, indicating a lack of independence of data points, which further reduces the limited degrees of freedom.

It is also important to realize that the concept of one single recruitment graph (deterministic approach) needs to be replaced by stochastic approaches that are based on probabilistic formulations of the endogeneous variables such as stock size variation, age structure variation, hence fecundity variation, etc. This is in contrast to exogenous stochasticity (i.e. forcing functions in terms of independent, random variations such as temperature patterns or turbulence-inducing events) which is useful for sensitivity analysis but otherwise usually of little value. The stochastic formulation allows for the possibility of expressing statements on recruitment in terms of probabilities.

Generally, a combination of the rational and empirical approaches allows a great amount of the limited information available to be incorporated. Often, the rational approach is used to generate hypotheses and to test and quantify those processes which can be measured or addressed experimentally. Then the empirical approach, i.e. experimental study, is used for testing, calibration, and verification. Further progress in fishery science requires advances in both approaches. A better rational, i.e. causal, understanding would allow us to predetermine the shape and properties of the function which will best describe the available data points. More data points allow a better and more detailed evaluation, revealing more aspects of functional relationships and thereby lead to increased understanding of the actual process involved.

Of course the classical rational method of hypothesis formulation and testing, leading to a mechanistic model, should be encouraged; however, it is recognized that useful application to real world problems will involve a considerable degree of integration of complicated process by means of simplified empirical transfer functions, i.e. simplified mathematical relations such as average values or linear equations.

A set of promising rational hypotheses are now available and these involve processes capable of exerting sufficient control on reproductive success such as to be discernible through the noise level of the multitude of additional processes. The following list is arranged in terms of physical processes, because both eggs and posthatch larvae are very much part of local physical processes, with the four categories containing results of recent research activity and interest and which are considered very promising avenues for further research.

(a) Vertical stability processes — Recent work (Lasker 1975; Hunter and Thomas 1974; IOC Workshop Report No. 28) has indicated a dependence of larval feeding success on fine-scale layers of food particles. These layers can be destroyed by vertical mixing (Kullenberg 1976; Owen 1981). Information on the structure, accumulation rate, nutritional suitability, and resistance to dissipation of such layers is required. The processes of sighting, approaching, attacking, and capturing appropriate prey organisms by larval fish take place on the microscale (millimetres to centimetres) and are believed to be strongly affected by turbidity and turbulence conditions. The interaction of water column stratification with turbulence generation is a key problem area. It is necessary to know how to formulate available wind data to indicate space–time windows sufficient for reproductive success (Bakun and Parrish 1981).

(b) Horizontal advection — Reproductive strategies often appear to be keyed to larval drift or passive transport mechanisms (Parrish et al. 1981). Larvae must be able to reach favorable nursery grounds. There appears to be a pattern of strong avoidance of offshore loss of reproductive products in the reproductive characteristics of stocks of coastal upwelling regions. Reproduction in areas of closed gyral circulation appears to be common. Where spawning is distributed in time and space or the larvae occur in the plankton over substantial time periods, very short-scale flow variations may tend to be integrated by the continuum of drifting larvae; thus a simple Ekman–geostrophic flow description may be adequate. Research on the use of established time series, such as sea level measurements or standard meteorological analyses, as indicators of flow variations should be encouraged. Variations in exchange of localized gyral circulations, which appear to be utilized in spawning strategies, within the larger-scale flow system should be investigated.

(c) Temperature — Rates of biological processes are controlled by temperature; extreme temperatures can be lethal. Thus temperature can usefully be used to define limits of occurrence. Anomalous temperature conditions, by changing growth or maturation rates, can cause disruptions and mismatches in time of critical life cycle events. A commonly cited example is the necessity for the production cycle of suitable food organisms to overlap with larval food requirements. In addition, temperature is a readily measured signal of important ocean processes (for example, in eastern boundary current regions, cool sea temperatures are often related to coastal upwelling and to horizontal advection from higher latitudes).

Temperature time series (depth profiled) which are characteristic of the space scale of reproduction are needed. Estimates of probable error are also required.

(d) Surface convergence or divergence — Horizontal structure (patchiness of larvae and their food organisms) is affected by convergence or divergence and associated frontal formation (Simpson and Hunter 1974; Owen 1981). Food availability and vulnerability to predation may increase in convergent fronts. Wind-driven Ekman divergence or convergence, which is controlled next to a coastal boundary by the alongshore wind stress and in the ocean interior by the wind stress curl, determine the vertical advection (upwelling or downwelling) in the upper ocean. Ekman suction and pumping can change slopes of ocean density structure and thereby alter current patterns. For example, in the California Current system the wind stress curl distributions coincide with the subpopulation structure of the major pelagic fish species (Parrish et al. 1981). This might also be the case in other areas.

Time series of ocean surface divergence processes and patterns should be developed and interpreted in a biologically relevant sense (Parrish and MacCall 1978). Error estimates are a particular requirement because a gradient of uncertain flow velocities is involved; errors are amplified in a derivative field of this sort. Horizontal mixing which would destroy spatial structure should be investigated. Linkage of frequency and intensity of frontal occurrence with large-scale surface convergence needs to be demonstrated.

The list could certainly be continued. For example, solar radiation is important to the production cycle as well as being a dominant stratification and turbulence energy source (i.e. winds). The biological interactions and their relationships with the physical variations should be studied. Any increase in rational understanding will allow better use of the very limited degrees of freedom in the available data.

Comparative studies appear a promising avenue for increases in understanding of processes that are difficult to address experimentally. For example, if there is a pattern of spawning by analogous stocks in semienclosed coastal gyres, one can reason that natural selection has operated to generate the pattern. Because natural selection implies reproductive success of preadapted individuals, it would be reasonable to assume that subsequent confinement of reproductive products within such a gyre is indicative of a significant survival factor. This provides a logical basis for development of a time series of variations in the strength of the gyre as an explanatory variable to be included in an empirical model and from which the contribution of such phenomena might be evaluated.

Explanatory index series should probably always be tailored to the scale of the reproductive process involved, although minimum scale may be dictated by data availability. Where possible they should be associated with a data source that can be continued for a reasonable period and preferably be hindcast over past periods of fishery operation. Thus experiments and new types of technology will be most profitable where they can be used to 'calibrate' an existing time–series data source. Time scales of interest will correspond to spawning frequencies, although the controlling factor may be rather short-scale events; for example, in the case of the effect of wind mixing on larval anchovy first-feeding success, a relevant series would be the interyear variability of the occurrence of space–time 'windows' during which storm events above a certain threshhold intensity are absent (Lasker 1975; IOC Workshop Report No. 28, 1981, p. 15–104).

Stage II — Juveniles — Juveniles are here defined as young fishes, from metamorphosis to those stages where they live in the same place (time and space) as the adults and become available to fishing.

Little is known about this stage even in well-studied areas because: (a) there is a lack of good gear for sampling them; (b) they do not usually occur where the adults and the larvae occur.

It is at the juvenile stage that the 'fine tuning' of the recruitment numbers occurs. During this stage the fish actively move into the area occupied by the adults, where they must learn to survive or in which they must establish a territory, e.g. as in coral reefs. As compared to the situation in the larvae, where starvation or predation might be viewed as largely nonselective, predation on juvenile fishes may have a strong 'selective' component, with mainly unfit or smaller, slower growing fishes being removed from the system.

Juvenile growth is often seasonal (Brett 1979; Ricker 1979). Fish typically spawn prior to the onset of a "growth season." Thus, ambient temperatures and anomalies have a strong effect on juvenile growth and on the resulting length of time they stay in size-related predator fields, which are themselves temperature-dependent. Density-dependent growth is often evident at this stage.

Problem-solving for this stage will also follow a pattern of rational understanding of processes including testing and calibration against empirical data similar to that described for Stage I.

Example hypotheses of particular interest are:

a) that recruitment is limited by niche availability in the case of reef fishes;

b) for demersal fisheries an important hypothesis would be that predation by adult demersal fish is a strong and varying source of juvenile mortality which modulates recruitment;

c) for upwelling systems hypotheses about predation and mortalities related to advection need to be tested.

Research requirements would therefore differ among these various systems. A common problem, however, is the general lack of suitable gear for sampling this stage of the life history and development of suitable gear would seem urgent. The study of the ecology, distribution, movements, and interspecies interactions of juvenile fish (especially of commercial species) could help in closing a gap in our understanding of fish population dynamics, especially in establishing whether there are monitorable mechanisms which contribute to the suggested 'fine tuning' of recruit numbers, of which the order of magnitude will likely have been determined during Stage I.

Data requirements need to be closely related to the timing and scales of distribution of posttransformation small fish patches. These vary from metres to kilometres and have time scales of perhaps weeks to months. General ocean circulation patterns may be useful in developing an understanding of this life history stage. Distributions are in some cases localized and the causes of this need to be explained by examining features of the physical oceanography (fronts, gyres, etc.).

Stage III — Non-reproductive adults — Stage III is defined as the non-reproducing adults, including juveniles or maturing stages which have recruited into an exploited resource.

Although fishery biology is at its best when adult fishes are discussed, there are several areas where the OSLR Programme could help gain new insights, generate new hypotheses, and provide opportunities to test them. These relate to:

a) The spatial distribution of fish, i.e.:

  i) with regard to fishes currently considered more or less limited to certain characteristic marine habitats (e.g. tuna species, or age-classes within species);

  ii) with regard to the general rule that bigger (often, but not necessarily older) fish of a given species tend to occur in water deeper and/or cooler than the smaller (often younger) stages.

In both cases explanations have been provided which relate the temperature and depth of occurrence and/or water mass characteristics, including particularly oxygen content.

b) The natural mortality of fish. Natural mortality comprises both species-specific endogenous properties as well as exogenous causes, and both may be linked with environmental temperatures (and anomalies), and certainly with changes in the biological milieu.

c) Growth is strongly temperature-dependent, and both the zoogeography of fishes (occurrence of various species at various places — long-time scale) and the growth parameters at a certain time of a given stock (short-time scale) can be linked to changes in ambient temperature. Temperature would thus influence such things as population structure, size at first spawning, and fecundity and quality of gametes.

The OSLR Programme, by refocussing attention on the influence of long- and short-scale oceanographic phenomena on adult fish could help explain adult distribution, abundance and vulnerability to fishing gear (availability), and many growth-related phenomena (e.g. maturation, migration).

Stage IV — Maturing and spawning adults — Stage IV in the life cycle of fishes is defined by the onset of the reproductive cycle in the adults. On a population level this cycle can be seasonal or continuous. Recent observations, on *Engraulis mordax* for example (Hunter and Goldberg 1981), confirm the continuous population spawning (or batch spawning of individuals). The "fecundity" of such species thus becomes a concept that is difficult to evaluate. This single parameter, fecundity, has often been used to calculate biomass of spawners from egg and larval survey data. It is important, therefore, to investigate more thoroughly the ability of populations to spawn continuously, and individuals repetitively.

There is little known regarding internal and external clues which initiate egg differentiation and maturation. Several effects appear to be related to temperature, among these differences in egg size and 'fecundity.' The thermal history of the juveniles and adults prior to Stage IV results in varying growth parameters and subsequently in varied fecundity, egg quality, and size. There are also apparent size−age effects on time of spawning and egg quality which are independent of temperature.

Little is known about how fish identify appropriate areas or locations for reproduction. There are several alternative strategies ranging from continuous sowing of gametes over the spawning season, to discrete, short-term spawning events (Sharp 1981).

Predation and Other Interactions Between Species

Species interaction is mainly caused by predation which here is interpreted in the most general sense, including man as the climax predator (Laevastu and Larkins 1981; Clepper 1979). Most management questions in some way relate to the concept of species interaction because it is only few stocks that, in practice, can be considered as isolated.

Our ability to predict short-term (1 yr) changes in stock composition to a large extent depends on our understanding of the mechanisms that govern predation on postrecruits. Possibilities of making probabilistic predictions of long-term (1−10 yr) changes in the stock compositions depend on our understanding of the predatory mechanisms as well as of recruitment.

Quantitative knowledge of predation mechanisms is still scarce, in particular, for the egg stage, the larval stage, and the juvenile stage. It is imperative, therefore, that as much information as possible on predation is extracted from available stomach content data. The few available stomach data sets can be used for making population level inferences in the sense that the stomachs from specimens of the same size sampled over broad areas and extended time represent predators that have been feeding in different geographic habitats. Data on the accessibility of various prey types during foraging is equally important as data on actual prey selection (stomach contents) to infer properties of the mechanisms governing food selection. Thus, stomach data sets, in particular for pelagic species, should be evaluated along with corresponding ecological data sets from the appropriate habitats. Approaches to bypass this problem are being developed based on Virtual Population Analysis or Cohort Analysis extended to account for species interaction (J. G. Pope, ICES CM 1979/H:16, ICES CM 1980/G: 19, unpublished data). There, total mortality for each entity of prey is partitioned into fishing mortality and natural predation mortality, and a 'residual' mortality (a coefficient accounting for mortalities due to causes other than predation).

Natural predation mortality is the fishery independent part of predation mortality, and is calculated by evaluation of an interlocking series of Virtual Population Analyses. This approach is necessarily based on various assumptions regarding the monthly or annual food consumption of each predator type (species, age, and size group) to reduce the number of unaccounted for variables.

Realistically, multispecies Virtual Population Analysis is a retrospective estimation of stock sizes that are in accordance with the observed stomach contents information. Evaluational classification of the relative importance of the various underlying assumptions is needed. For example, the derivation of reliable selectivity indices should probably not be done exclusively based on stomach data. This would require a prohibitive amount of stomach sampling. There is a need to combine the empirical approach with rational models of size selection (Beyer 1980). The only hypotheses presently available refer to size selection. One is the Andersen and Ursin (1977) log-normal selection model. There, it is assumed that a preferred prey size exists and that the ratio of predator size to preferred prey size remains the same throughout a predator's lifetime. This log-normal size-selection model is completely specified by two parameters — the relative measures of preferred prey size and selectivity broadness. No general hypotheses seem to be available with respect to interspecific differences in vulnerability to predation. Differences in vulnerability or desirability may be caused by differences in the external protective structures and avoidance behavior of the potential prey types.

Rational models will help in identifying data requirements and designing experiments on various scales to improve understanding of species interaction as well as help in utilizing the already available information on predation.

The complete story of predation is about why most fish die and why some of them survive. Predation is simply a sequence of perceptions, decisions, and actions of predators about their prey. This is, however, oversimplified. Apparently predators often encounter prey organisms one at a time. Their feeding strategy and success depends on several factors including their state of hunger, experience or skill level, adaptation to certain prey types, and probably many other factors apart from their size or species. Filter feeders depend on similar recognition and reaction to their prey, depending on their hunger state and other stimuli.

The degree to which it will prove necessary to distinguish between different predators — sometimes considered as identical — and to incorporate knowledge of their various feeding strategies depends on the marine ecosystem in question and the nature of the problem to be addressed. At present, however, it is not even clear what the basic differences in feeding strategies are that allow closely related species to coexist. In the first instance, there is a need for observations of individual feeding behavior. This type of process-oriented data collections must to a large extent be carried out *in situ* for juvenile and adult fish. Additional studies in tanks or enclosures of sufficient size to avoid behavioral or activity constraints may help in clarifying concepts. Other fields which clearly require more experimental studies are digestion and gastric evacuation. Basic principles of the digestive process are not yet understood and this limits understanding of the relationship between stomach contents and actual food consumption.

The possibilities of evaluating causal aspects of vulnerability to predation by comparing characteristics (e.g. condition or parasite burden) of freshly caught prey found in the stomach with live prey of the same characteristics, i.e. specimens of the same length, could prove important.

In the early life history stages experimental studies may be of considerable help in identifying feeding mechanisms, requirements, and limitations for growth and survival. These studies would be most informative if performed in simulated mini-ecosystems (or laboratory microcosms). This, among other things, requires the ability to measure and perhaps control the species, size, and spatial distribution of plankton. Nearly all experimental studies with larval fish have been carried out at food densities in great excess of what is usually found by integrative measurements taken in the sea via nets, pumps, or other techniques. Intensive studies of growth and survival of larval fish, with and without larval predators, with interpatch zooplankton densities in the order of 10 plankton per litre are needed. To be useful such studies need to be carried out so that there is enough data collected to permit alternative, statistically testable hypotheses on growth and survival to be resolved. This is not possible with current measuring techniques. Techniques are needed for precise and automatic detection and monitoring of local (centimetre to metre scale) densities and sizes of plankton (10 μm−3 mm) and fish larvae (3 mm−30 mm) without disturbing the system. The usefulness of optical or acoustic techniques for this purpose — for application both in the laboratory as well as in the field — needs further investigation.

Major Systems of Interest

Systematic ordering of the stages in the life cycles of fishes leads directly to scaling problems and to questions of appropriate research methodologies which might be used to study these different stages and scales. There are other important considerations which are also very restrictive in the sense of scaling and approach, namely biogeographic or ecosystem considerations. In the higher latitudes, which have been purposefully deleted from detailed discussions, seasonality of production is the dominant variable, with a resultant selection in evolutionary contexts for annual cycles and longevity in the dominant fish species. In the tropical and subtropical regions a full spectrum from seasonal to nearly continuous production patterns are observed. Also, much of the biomass comprises large numbers of small, short-lived, rapidly responding species (Pauly 1979), whereas the larger, longer-lived species, although present, tend to be of relatively low abundance in most systems, because of their relatively high position in trophic webs.

In an attempt to focus attention on systems likely to be important to developing countries, four basic regimes were selected as representative of characteristic habitats. Certainly there are distinct differences among the several manifestations of these types or systems, but because of overriding physical biological effects, similarities have emerged which make generalization within each type of system possible.

UPWELLING SYSTEMS

The upwelling regions of the world are characterized by high productivity and massive pelagic fish stocks which exhibit extreme fluctuations. Recent research indicates that coastal upwelling can be driven both by local wind forcing and by disturbances propagating from elsewhere. On experimental time scales (fractions of a day to several weeks), propagated effects seem to contribute relatively greater variance in tropical systems than in subtropical or temperate systems. Thus the collapse of the California sardine stock has occurred in a system that appears to be predominantly locally wind-driven. Collapses of the anchoveta in the Peru Current, and the sardinella in the Guinea Current, have occurred where at least the shorter-term fluctuations are uncorrelated with local wind variations.

The upwelling system off southwest India appears to be an extreme case of noncorrespondence to local wind forcing. Here the upwelling season coincides with the southwest monsoon, when the prevailing wind tends to be directly toward the coast. Thus the offshore surface Ekman transport which would drive locally produced upwelling actually vanishes at the very season when upwelling is most evident. Possible explanations include coastal trapped wave propagation around the southern tip of India from an area of offshore-directed surface transport on the east coast. It is also possible that the Somali Current circulation, which leads to a southwest current off southwest India during the southwest monsoon, may be contributing to the observed upwelling through interactions with bottom topography (onshore-directed bottom Ekman layer, etc.). The stock of oil sardine off southwest India has been subject to extremely wide long-period variations, appearing in such large numbers during the upwelling season as to constitute the major single-species fishery resource during certain groups of years, while being virtually absent over other multiyear periods.

The particular massiveness of the fish stocks inhabiting upwelling regions suggests that upwelling is a basic mechanism in maintaining them. Most of the recently developed understanding of the dynamics of upwelling systems concerns the shorter time scales which are most readily addressed by experiments. However, the observed stock variations occur on long (seasonal and interyear) time scales. Even off Peru, the Coastal Upwelling Ecosystem Analysis (CUEA) studies suggest that the quasisteady upwelling which may underly the energetic shorter scale fluctuations may actually be locally wind-driven. Understanding longer term variations in the upwelling system could lead to insights into the interacting effects of exploitation and environment on stock variations which would yield improvements in the management and exploitation of these resources.

CORAL REEFS

Coral reefs contribute significantly to the world's total fishery catch. Yet the overwhelming part of coral reef research is ecologically oriented and conducted predominantly by marine biologists, ecologists, and ethologists, with very little input going into applied questions relevant to fishery biology and resource management.

Among the more urgent questions pertaining to the exploitability and long-term productivity of coral reefs are those relating to the recruitment of young fish to the coral reef populations. In this context, emphasis should be given to the separation of reef systems which produce their own recruits from those which receive their recruits from neighboring reef systems, and to the transport mechanisms by means of which recruit transfers take place. Answers to these questions, which could help in the identification of suitable areas for underwater national parks or broodstock reserves, would be of considerable interest to countries whose reef resources need protection. An interesting question for fishery science would be an assessment of the range of influence of such reserves.

The study of the interactions between coral reef fishes could also help in elucidating the process of predation and its possible role in stabilizing and structuring reef populations. The study of fish predation in reefs would also help to answer questions pertaining to energy transfer between trophic levels and to the role of large predators in relation to a fishery.

Likely areas in which to conduct such research are the Caribbean, where previous research has laid a solid groundwork to start from, and the Great Barrier Reef, where the replication of experiments would seem easiest.

TROPICAL AND SHELF DEMERSAL FISHERIES

Catches from tropical shelf demersal fisheries are characterized by large numbers of species. There is great difficulty in obtaining fisheries data at the species level. In some areas research surveys have provided useful time series of abundance changes by species groups and these suggest a greater stability with respect to the environment than temperate systems exhibit. This may, however, be simply an impression created by ignorance of such factors as recruitment or catch of each species, or even due to the behavior of the fishermen themselves.

The development of fisheries research in these areas will probably be dominated by surplus production models for some time in the absence of data for more analytical approaches. An approach to analytical techniques may be made by estimating growth, mortality rates, and recruitment for certain representative species. Until this is done, it may be premature to initiate major programs aimed at understanding the biology of, for example, the early stages of the life history.

More pressing scientific problems would seem to be a comparative study of the factors that effect productivity (primarily of fish) in these areas. A comparative study might, for instance, be carried out in the South China Sea area with the aim of explaining abundance or yield in terms of environmental features. Because the demersal fisheries there seem to operate in semiestuarine systems, it seems probable that runoff may be a key factor. Such a study might enable surplus production modeling applications to be generalized over this area and might also enable species successions resulting from fishing pressure to be predicted. The time scale of such an investigation might be by month and the size scale by about 50-nautical-mile lengths of coast. These scales would doubtless need to be adapted to fit with topographical details.

Results from the Gulf of Thailand, Indonesia, and elsewhere suggest that fish stocks in the area may be rather localized. Various groundfish surveys indicate different trends in abundance in different areas. If the fisheries in such areas are based on various small substocks this will have important implications for the management of these fisheries. Scientific studies of stock divisions in such areas may therefore be of value. Tagging/meristic/genetic studies would seem indicated in the first place but studies of ocean circulation processes and larval transport may be indicated to back these up. The size scale of these studies might be of the order of 100–200 nautical miles of coastline.

Certainly given the contribution of mangrove and other brackish-water systems to coastal fisheries, a tremendous research effort is required to evaluate the dynamics and dependencies in these complex ecosystems which affect subsequent production. Here again, scale will be of great importance.

OCEANIC PELAGIC FISHERIES

The oceanic environment is perplexing in that there are many broad provinces with physical–chemical–climatic properties which can be labeled, but the occurrence of resource is patchy within these provinces. The major apparent abundances and vulnerability zones of the resources are often at interfaces of the physical–chemical provinces, including the thermocline. There are examples of unconventional resources which have recently come to our attention (e.g. Antarctic krill, mesopelagics off Oman).

There are undoubtedly others. With ever-increasing insights arising from marine exploration (for example, recent location of deep-water thermal and freshwater vents), new potentially interesting sources of productivity are being identified, and in some cases commercial species are found associated with them. Often only the knowledge of the sources of the productivity helps to dispel some of the uncertainties in fishery resource contexts.

Important questions still exist about the transfer of energy in deep ocean systems to the larger, but not particularly numerous apex predators.

Tunas and their kin (the genera *Thunnus*, *Euthynnus*, *Katsuwonus*, *Auxis*) are special cases requiring specific modes of study. However, considering that they are presently under investigation by large bodies with diversified interests, other open ocean resources can be identified which should perhaps receive more attention. At least three — rainbow runner (*Elagatis bipinnulata*), dolphins (*Coryphaena* spp.), and oceanic sharks — seem to be of sufficiently greater potential commercial interest than presently exhibited that they certainly warrant further attention in this context.

The deployment and monitoring of open ocean-aggregation devices for the explicit purpose of concentrating relatively diffuse, but not particularly abundant individuals or small schools of oceanic predators (including the species mentioned above) could provide both scientific insight into aggregation cues and improved utilization of these resources. In a broader context, studies of these predators' behavior and ecological properties could also help in determining their impact on pelagic and coastal ecosystems.

Suggested Studies

Two approaches to fishery/environment studies are possible — detailed studies of particular situations (e.g. anchovy in the California current), and comparative studies of similar systems (e.g. coral reefs). The latter has two aspects. There is the direct practical aspect in which a fishery scientist working in a poorly studied area can obtain some insight into how his or her questions might be answered (and possibly also some of the answers) by analogy with a better-studied area. The other is of more general scientific interest and results from examination of data from a number of similar systems (no one of which may have been studied in depth) to identify patterns and differences and thus obtain insights into how each system operates.

These approaches are all valuable, but it is important that a proper balance is maintained. In particular the Group felt that it was vital to have high quality in-depth studies of at least some representative examples of each of the main systems discussed in this report. Such studies cannot be done for all examples in each system and some selection must be made. In the context of OSLR it is fortunate that there are examples of most systems of interest to developing countries off the coast of, or close to, developed countries with high-quality expertize in the marine sciences (eastern boundary currents off California and Portugal/northwest Africa; coral reefs off northeast Australia; tropical shelves in the Gulf of Carpentaria and the Gulf of Mexico). Many of the necessary detailed studies might well be conveniently carried out in these areas. Participation by scientists from developing countries in these studies should be encouraged and facilitated, e.g. through cooperative research programs and fellowships, though this should not rule out the execution of detailed studies off developing countries where sufficient expertize can be brought to bear. At the same time assistance should be given to developing countries with respect to their own systems, especially in the compilation and analysis of data that might be used in comparative studies, and in the identification, formulation, and pursuit of relevant research topics.

Access to Data

The participants noted the instructions to the IOC Secretary (IOC Resolution XI-17 to "...develop through correspondence an inventory of information..." on subjects of marine ecosystems.

Dissemination of data and information is not a new problem, but the multidisciplinary studies that will be required in OSLR add a new dimension to the problem. Not only must, for example, data on physical oceanography be available to fishery scientists, but they should be available in a form that the fishery scientist can readily interpret and employ by combining it with fishery data to study the effects of varying environment on fisheries. The same is true as regards the possible use of fishery data by oceanographers and others.

Many of the basic environmental data (e.g., sea surface temperatures) can be located through the World Data Center System, the IOC Marine Environmental Data Inventory (MEDI), and both national and regional oceanographic data centers; marine meteorological and climatological data can be obtained through the World Data Center System and the World Meteorological Organization (WMO).

The products of these data centers are often not in the form that a fishery scientist can conveniently use, even when the figures presented are the ones of interest. There is a need for presentation of the relevant oceanographic data in a form and on a time and area scale that are directly applicable to fisheries. It might be a later task of OSLR to identify more closely what the relevant data and the appropriate time and area scales are, as well as to identify the locations where such data would be most useful. In addition to the basic data stored in the Data Centers there are quantities (e.g. wind stress curl) that can be derived from these — and may be directly relevant fo fisheries, but which are not generally available. These need to be calculated, and an appropriate format will be required for each study program depending upon time–area scales of interest.

The problems of making fishery data available to nonfishery scientists are even more difficult. Basic fishery statistics (particularly of fishing effort and corresponding catch) are the most widely used source of data in monitoring the abundance of fish stocks. However, the interpretation of the types of data generally available is full of potential pitfalls (much of the work of fishery scientists is concerned with the suitable adjustment and interpretation of this type of data) so that they are not generally suitable for direct incorporation in data centers, to be used by the unwary without further guidance. Nevertheless, there is a large volume of fisheries data which could be most useful to environmental scientists if they were aware of them and could be guided in their use and interpretation by someone familiar with the fishery concerned. It was therefore suggested that it would be useful if a catalogue or inventory of such data could be developed (perhaps by FAO), setting out for each country and fishery for which data series exist: the nature of the fishery (major species and methods of fishing), the period over which data exist; the nature of the data (e.g. units of fishing effort used); the form in which the data are recorded (e.g. annual statistical reports, unpublished notes, files on magnetic tape); and the institution to which enquiries should be addressed.

Concluding Remarks

Regional or fishery scale multidisciplinary scientific fora for the exchange of information, formulation of projects, and coordination of activities will be of primary importance to the success of the OSLR programs. Equally important will be the individual and institutional efforts necessary to disseminate and apply existing knowledge and techniques for resolving questions relevant to living resources. These efforts need no further justification; what is needed is dialogue and action.

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TURBULENCE, TRANSPORT, AND PELAGIC FISH IN THE CALIFORNIA AND PERU CURRENT SYSTEMS

ANDREW BAKUN AND RICHARD H. PARRISH
Pacific Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service
P.O. Box 831
Monterey, California 93942

ABSTRACT

The California and Peru Current systems are compared in terms of three environmental processes thought to be likely regulators of reproductive success of pelagic fishes: (1) turbulent mixing, leading to destruction of fine-scale food strata required for successful first feeding of larvae, (2) offshore transport, resulting in loss of reproductive products, and (3) upwelling intensity, as it relates to total productivity of the system. Newly generated climatological distributions of coastal-oceanic temperature contrast, wind-generated turbulent energy production, sea surface wind stress, and surface Ekman transport are presented. A consistent pattern of avoidance of centers of maximum upwelling, which are characterized by intense turbulent mixing and offshore transport, is noted in the reproductive strategies of anchovies. Large stocks tend to occur in regions of low turbulent mixing, downstream of upwelling maxima.

RESUMEN

Se comparan los sistemas de corrientes de California y Perú en relación con los procesos ambientales estimados como reguladores del éxito en la reproducción de los peces pelágicos: (1) la mezcla turbulenta que elimina los estratos conteniendo organismos de talla pequeña, necesarios para un umbral óptimo en la alimentación de las larvas; (2) flujo mar afuera que ocasiona pérdida de gametos y productos de la reproducción; y (3) la intensidad del afloramiento y su relación con la productividad total del sistema. Se discuten las características climatológicas en relación con el contraste en la distribución de la temperatura en la zona oceánica y costera, la turbulencia generada por el viento, la acción del viento sobre la superficie del mar, y el transporte Ekman en aguas de superficie. La estrategia de las anchovetas durante su época de reproducción muestra una caracteristica constante. Así, evitan los centros de afloramiento máximo donde se produce una acción de mezcla intensa y turbulenta, y las zonas de corrientes mar afuera. Las poblaciones tienden a concentrarse en regiones donde la acción de mezcla y turbulencia es de intensidad baja, en la corriente procedente de las zonas de máxima surgencia.

INTRODUCTION

The four major eastern boundary current systems of the world—the California, Peru, Canary, and Benguela—appear to have similar environmental dynamics and are dominated, in terms of exploitable biomass, by very similar assemblages of pelagic fish species (Table 1). Bakun and Parrish (1980) presented a rationale for interregional comparative studies as a means for developing insights to enhance effectiveness in managing fishery impacts in the face of fluctuating environmental conditions.

The economic importance of the stocks of pelagic fishes in the four principal eastern boundary currents and their apparent tendency to collapse under heavy exploitation make it of great interest to know to what extent we can transfer experience from one system to another, i.e. whether to expect similar outcomes from similar actions. For example, in the Peru Current system a massive anchovy-dominated system has, under heavy exploitation, recently shifted to a sardine-dominated system. The presently expanding exploitation of the central stock of California Current anchovy invites comparison of the two situations. Conversely, extremely heavy exploitation of sardine, jack mackerel, and mackerel resources off Peru and Chile is reminiscent of the heavy exploitation of similar California Current stocks, followed by collapse and subsequent shifting of the system to anchovy dominance several decades ago.

Deducing the environmental factors controlling reproductive success through pattern recognition of environmental-reproductive relationships derived from different eastern boundary current systems is one method to integrate the oceanographic and fishery research that has been carried out in the different regions. Reproduction is singled out as the most significant life-history feature because recruitment variability is considered to be the principal factor responsible for pelagic fish population fluctuations in upwelling regions (Troadec et al. 1980; Csirke 1980; Lasker 1981). Natural selection implies that observed reproductive

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TABLE 1

Dominant Anchovy, Pilchard, Horse Mackerel, Hake, Mackerel, and Bonito in the Four Major Eastern Boundary Currents

California Current	Peru Current	Canary Current	Benguela Current
Engraulis mordax	*Engraulis ringens*	*Engraulis encrasicholus*	*Engraulis capensis*
Sardinops sagax	*Sardinops sagax*	*Sardina pilchardus*	*Sardinops ocellatus*
Trachurus symmetricus	*Trachurus symmetricus*	*Trachurus trachurus*	*Trachurus trachurus*
Marluccius productus	*Merluccius gayi*	*Merluccius merluccius*	*Merluccius capensis*
Scomber japonicus	*Scomber japonicus*	*Scomber japonicus*	*Scomber japonicus*
Sarda chiliensis	*Sarda chiliensis*	*Sarda sarda*	*Sarda sarda*

After Bakun and Parrish 1980.

strategies represent successful accommodation to the most crucial environmental factors. Thus, compelling patterns in seasonal and geographical relationships of reproductive and environmental characteristics suggest important causal linkages over the period during which the reproductive characteristics were generated. The assumption that these same linkages continue to affect reproductive success on a year-to-year basis provides a rational basis for including these factors in empirical modeling efforts.

Recent studies have directed attention toward three classes of environmental processes considered to be likely regulators of pelagic fish reproductive success.

1. Destruction of fine-scale food particle concentrations by wind-generated turbulent mixing has been found detrimental to larval anchovy survival by a series of laboratory and seagoing experiments (Lasker 1975, 1978; Lasker and Smith 1977). Comparative studies of anchovy reproduction in the California Current system versus turbulence and water column stability (Husby and Nelson, this volume) have added corroborative evidence.
2. A comparative study of seasonality and geography of ocean transport and fish reproductive strategies in the California Current (Parrish et al. 1981) has indicated a general pattern of avoidance of intense offshore flow conditions in the reproductive habits of a wide variety of coastal fish stocks. The suggestion is that offshore loss of reproductive products may exert an important control on reproductive success.
3. The major upwelling regions of the oceans are notable for high levels of primary organic production and for particularly massive fish stocks (e.g., Cushing 1969). Recognition of this pattern has led to the widespread belief that fish abundance in these regions is dependent on maintenance of organic production by the upwelling processes, and that long time-scale variations in upwelling intensity may induce fish stock fluctuations. Bakun and Parrish (1980) reviewed a number of recent studies in which estimates of variations in upwelling intensity in the California Current system have been related to fish stock variations.

In this paper we focus primarily on the first two hypotheses. The third is considered in terms of the linkage between offshore surface transport and coastal upwelling, the differing effects being distinguished according to the time and space scales on which they operate; for example offshore transport previous to and upstream of spawning activity might enhance larval survival by ensuring adequate food particle concentrations, whereas the same level of offshore transport right at the spawning site could result in offshore loss of eggs and larvae.

Offshore surface transport is adequately represented as Ekman transport (Parrish et al. 1981), except in the immediate vicinity of the equator. Actual transport is the sum of the Ekman and geostrophic components; however, we have not specifically addressed the

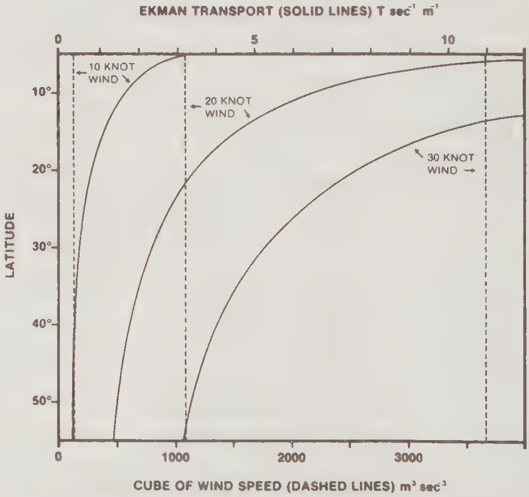

Figure 1. Turbulent mixing energy production (proportional to the third power of the wind speed) vs Ekman transport, for several values of wind speed.

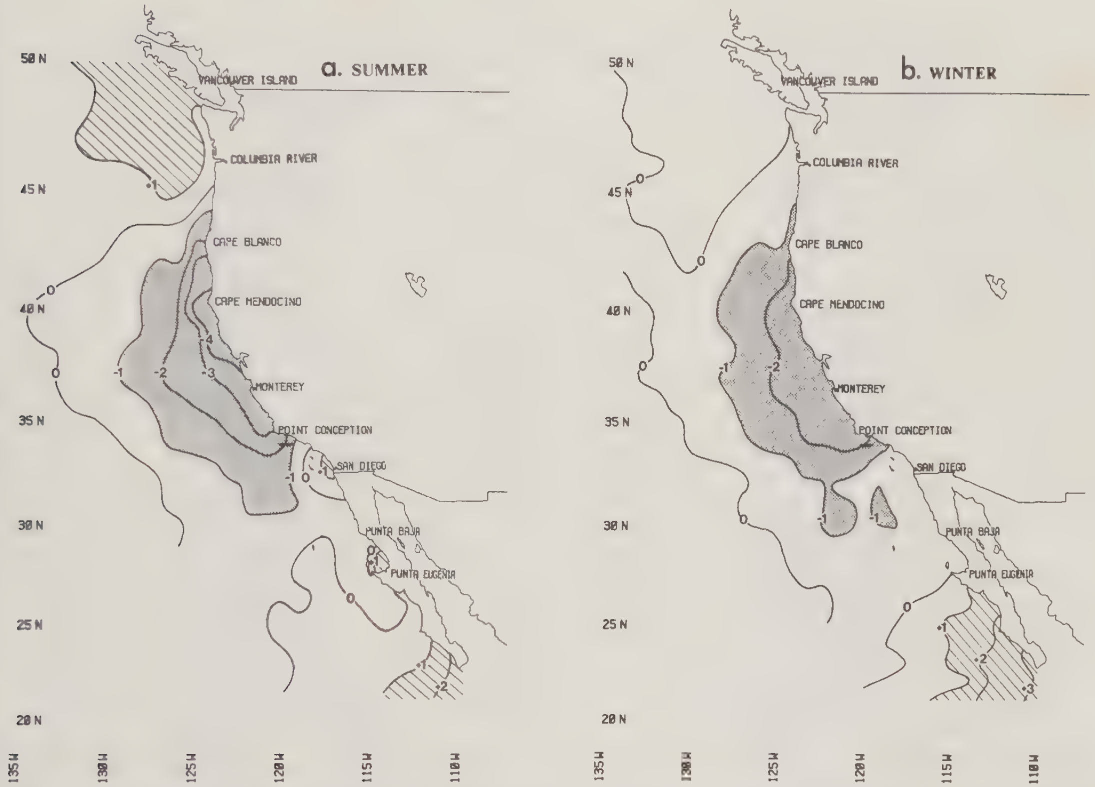

Figure 2. Coastal temperature anomaly (degrees Celsuis) computed as the difference between the temperature at each location and a smoothed reference temperature considered to be characteristic of offshore conditions at the same latitude (see text). *(a)* Summer (May, June, July, Aug.). *(b)* Winter (Nov., Dec., Jan., Feb.).

geostrophic component because Peru Current flow fields are not yet available on the proper scale. The rate of production of wind-generated turbulent mixing energy varies as the third power, or "cube," of the wind speed (Niiler 1975). Thus for a given wind speed, turbulent mixing energy production is not dependent on latitude, whereas Ekman transport has a strong latitude dependence (Figure 1). This difference is basic to our interregional comparison; for example, a given level of offshore transport would be accompanied by a much lower level of turbulent mixing off Chimbote at 10°S than in the Southern California Bight at 33°N.

SEA SURFACE CLIMATOLOGY

California Current Coastal Temperature Anomaly

Summer and winter distributions of coastal temperature anomaly for the California Current region (Figure 2) were constructed as follows. All the sea surface temperature observations available in the Fleet Numerical Oceanography Center's version of the National Climatic Centers' File of Marine Surface Observations (TDF-11) for each group of months were averaged by 1-degree latitude and longitude quadrangles. A smoothed offshore temperature reference was constructed by successively applying, at each 1-degree latitude increment, a 5-degree latitude by 3-degree longitude moving-average filter centered at the eleventh 1-degree quadrangular sample westward from the coast. To further minimize sampling irregularities, the three highest and three lowest of the fifteen sample averages covered by the filter at each step were discarded and the remaining nine averaged together; the result is a smoothly varying function of latitude, which we chose as a reference of the offshore oceanic temperature conditions. Finally, the value of this reference at the proper latitude was subtracted

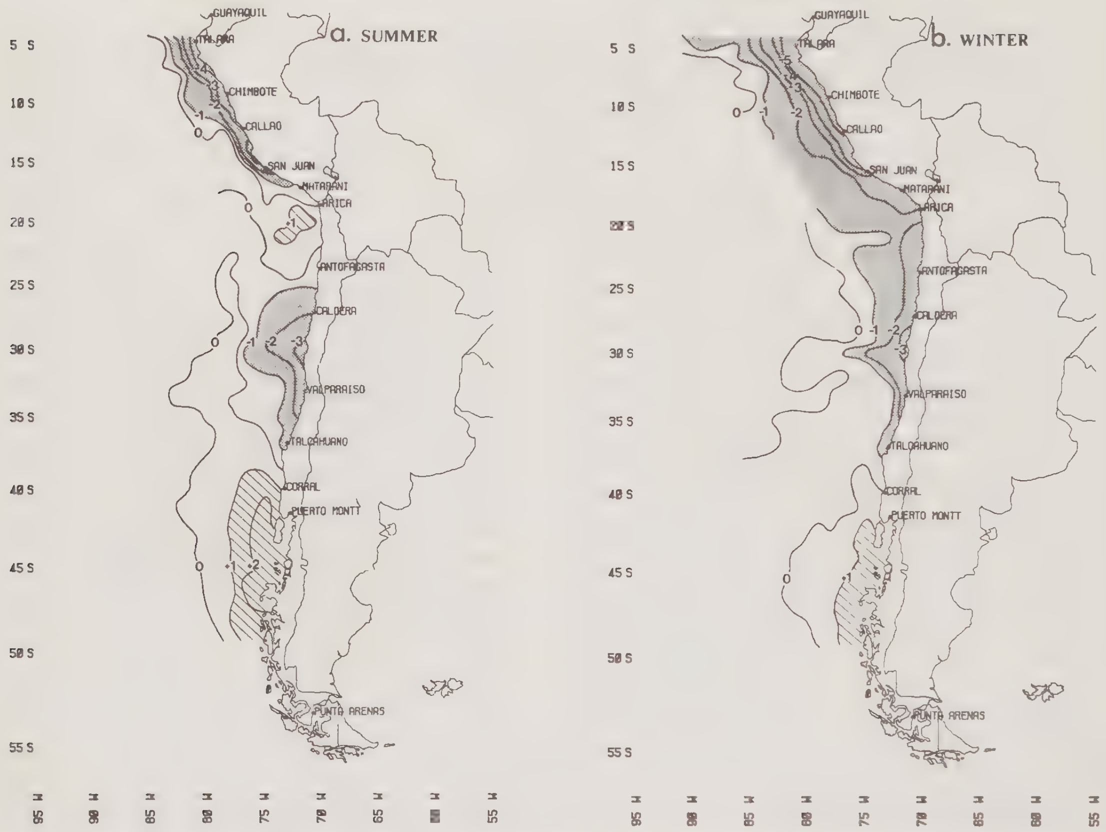
a. SUMMER
b. WINTER
GUAYAQUIL
TALARA
CHIMBOTE
CALLAO
SAN JUAN
MATARANI
ARICA
ANTOFAGASTA
CALDERA
VALPARAISO
TALCAHUANO
CORRAL
PUERTO MONTT
PUNTA ARENAS
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
55 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
60 W
55 W
0
-1
-2
-3
-4
-5

Figure 3. Coastal temperature anomaly (degrees Celsius) computed as the difference between the temperature at each location and a smoothed reference temperature considered to be characteristic of offshore conditions at the same latitude (see text). *(a)* Summer (Nov., Dec., Jan., Feb.). *(b)* Winter (May, June, July, Aug.).

from each 1-degree averaged temperature. Coastal temperature anomaly as used herein is therefore the difference between the temperature at each location and the large-scale temperature offshore; it thus filters the global scale equatorward temperature gradient, thereby highlighting local effects.

The area of negative anomaly greater than 1°C (shaded in Figure 2) delineates the area of maximum upwelling that is centered off northern California. The lobe of negative anomaly extending southward from Point Conception appears to be advective in origin, although local Ekman pumping (oceanic upwelling) associated with the strong positive wind stress curl in this location (Nelson 1977) may be a factor. During the summer, positive anomalies greater than 1°C appear in the interior of the Southern California Bight and within Sebastian Vizcaino Bay, north of Punta Eugenia (Figure 2a). Positive anomalies off the Pacific Northwest appear to be continuous with generalized warm advection into the Gulf of Alaska region. The area off Punta Baja has negative anomalies consistent with an upwelling region, but their magnitude is very low compared to the region north of Point Conception. The winter distribution (Figure 2b) is grossly similar to that for summer, but with a general lessening of gradients.

Peru Current Coastal Temperature Anomaly

The coastal temperature anomaly distribution for southern hemisphere summer (Figure 3a) off Peru and Chile indicates two distinctly separate upwelling maximum regions, one off Peru and the other off north-central Chile centered at about 30°S. These are separated by a region of warm anomaly near Arica.

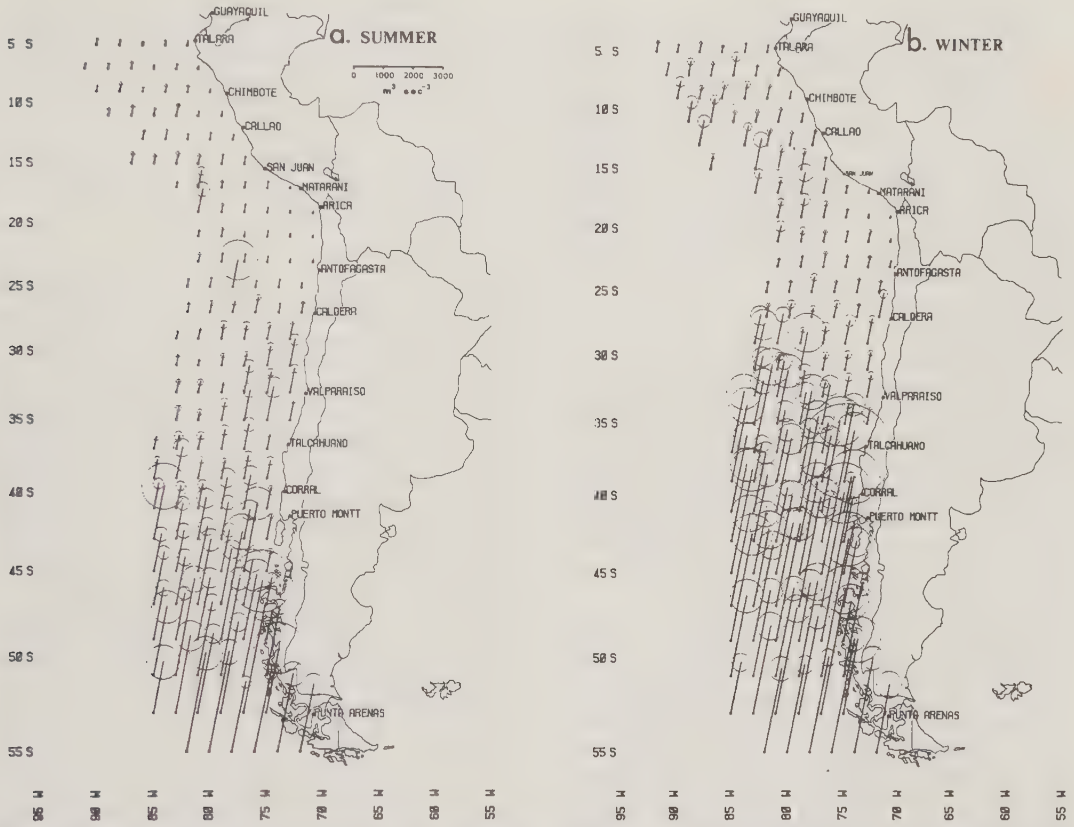
a. SUMMER
b. WINTER
0 1000 2000 3000
m³ sec⁻³
GUAYAQUIL
TALARA
CHIMBOTE
CALLAO
SAN JUAN
MATARANI
ARICA
ANTOFAGASTA
CALDERA
VALPARAISO
TALCAHUANO
CORRAL
PUERTO MONTT
PUNTA ARENAS
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
55 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
60 W
55 W

Figure 4. Cube of wind speed (m^3sec^{-3}) indicating rate of turbulent mixing energy production by the wind. Mean magnitude is indicated by length of each symbol; the standard error of each mean magnitude is indicated by the radius of the circle plotted at the top of each symbol (see scale on figure). *(a)* Summer (Nov., Dec., Jan., Feb.). *(b)* Winter (May, June, July, Aug.).

Water mass analysis (Cañon 1978) indicates distinctly different source waters for the upwelling occurring in the two regions. South of 40°S latitude, coastal warming is associated with warm poleward advection resulting from bifurcation of the mid-latitude west wind drift.

During the winter (Figure 3b) the coastal temperature anomaly off Peru is somewhat more intense than in the summer. The area of near-coastal warming off Arica disappears, but a definite minimum in the coastal temperature deficit continues to separate the two upwelling maxima. The negative temperature anomaly in the Chilean upwelling maximum appears to be slightly less intense in winter, as is the coastal warming south of 40°S. This smoothing of gradients in the coastal temperature anomaly distribution during winter relative to those in the summer distribution is similar to the situation noted for the California Current region (Figure 2).

Peru Current Turbulent Mixing Energy Production

One-degree summaries of wind reports were constructed from the same TDF-11 data file. In order to clarify the presentations in this paper, symbols are plotted only for alternate 1-degree quadrangles in both latitude and longitude coordinates. Thus only one-fourth of the total number of independent samples are shown. The South American coast is too large an area to indicate all the samples on a figure. The complete data set has been examined, and the reduced set shown illustrates the characteristic features. Where a particular sample contains fewer than ten observations, no symbol is plotted.

The distributions of the cube of the wind speed

(Figure 4) show much higher values in the south than in the north, with the region of extremely high values extending farther north in the Southern Hemisphere winter than in the summer. The regions near the coast are generally less turbulent than offshore; a notable exception is the Chilean upwelling maximum region near 30°S during summer. Low turbulence production is characteristic of the coastal region of Peru and of the extreme northern part of Chile, with summer being the least turbulent period. A spatial minimum of wind-generated turbulence is located within the coastal bight near Arica throughout the year.

Peru Current Wind Stress

The resultant stress of the wind on the sea surface is directed equatorward during summer (Figure 5a) along the coasts of Peru and Chile to 40°S. Moderate magnitudes characterize most of the coast of Peru; very low values occur within the coastal bight near Arica. Strong equatorward stress overlies the region of negative coastal temperature anomaly centered near 30°S (Figure 3), which is identified as the Chilean upwelling maximum. South of 40°S strong coastward stress is associated with large-scale westerly airflow.

During winter (Figure 5b) the equatorward stress off Peru strengthens substantially. The bight off Arica continues as a definite minimum in the distribution. The strong resultant stress found in summer near 30°S has disappeared; the offshore region at this latitude is under the influence of the westerly airflow, which has expanded northward. The "roaring forties" (the area south of 40°S) show magnitudes of resultant coastward stress similar to those in summer; however, relatively large standard error ellipses demonstrate stormy, highly variable winter conditions.

Peru Current Ekman Transport

The latitudinal variation in the Coriolis effect (Figure 1) modifies the distributional patterns when the stress distributions (Figure 5) are converted to Ekman Transport (Figure 6). Strong offshore transport is indicated off Peru, particularly in winter. Numerical magnitudes in this case should be viewed with caution because the Ekman transport relationship breaks down at the equator; it is presently unclear how close to the equator Ekman transport continues to acceptably approximate actual transport conditions.

The Chilean upwelling maximum near 30°S is associated with strong offshore-directed Ekman transport during summer (Figure 6a), which relaxes in winter (Figure 6b). Thus the seasonal Ekman transport cycle is similar to that in the Californian upwelling maximum (Parrish et al. 1981), but opposite in phase to that off Peru. The coastal bight near Arica appears as a region of minimal offshore transport, separating the two upwelling maximum regions and their associated intense offshore transport conditions. South of 40°S the Ekman transport is generally parallel to the coast and equatorward, with a definite onshore component south of about 48°S latitude.

ANCHOVY AND SARDINE STOCKS OF THE CALIFORNIA CURRENT AND PERU CURRENT SYSTEMS

Anchovy

Anchovies are among the most abundant fishes in eastern boundary current regions. In the Peru Current region the dominant anchovy is *Engraulis ringens;* a closely related species, the northern anchovy *(Engraulis mordax),* dominates in the California Current region. Both species are widely distributed; according to Cañon (1978) *E. ringens* ranges from 4°30′S to 42°30′S, and according to Miller and Lea (1972) *E. mordax* extends from 23°N to 53°N. Both species have extended spawning seasons, with some eggs and larvae being taken all year. Eggs and larvae occur over nearly the entire range of both species; however, they are heavily concentrated in distinct spawning grounds.

Meristic, morphometric, and tagging studies suggest that there are at least two major stocks of *E. ringens* (Tsukayama 1966; Rojas de Mendiola 1971; Jordán and Malaga 1972; Serra and Gil 1975). The bulk of the Peruvian fishery was based on a stock centered off northern and central Peru. A smaller stock centered off southern Peru and northern Chile was the basis of the Chilean fishery. Both of these stocks are currently greatly depleted. There is meristic and spawning-pattern evidence for a third stock near Talcahuano (36°S) in central Chile (Brandhorst, et al. 1965; Jordán 1980). A separate fishery has existed on this apparent stock and another pelagic species, *Clupea bentincki* (Serra 1978).

The Peruvian stock has its major spawning grounds located in northern and central Peru from 6°-14°S, and the highest concentrations of eggs occur near Chimbote at about 9°S (Santander 1980). Santander (1981) suggests that the areas and time of maximum spawning do not co-occur with the areas and periods of maximum upwelling; spawning is greatly reduced in the core of maximum upwelling (14°-16°S).

Cañon (1978) found several centers of spawning for the Peru-Chilean stock in northern Chile, especially near Arica (18-19°S) and Mejillones (22-23°S). However, the available literature does not indicate how far the spawning grounds extend into southern Peru. Anchoveta eggs have been found as far south as 40°S (Cañon 1978), and it is reported (Serra et al. 1979) that the spawning grounds of the potential central

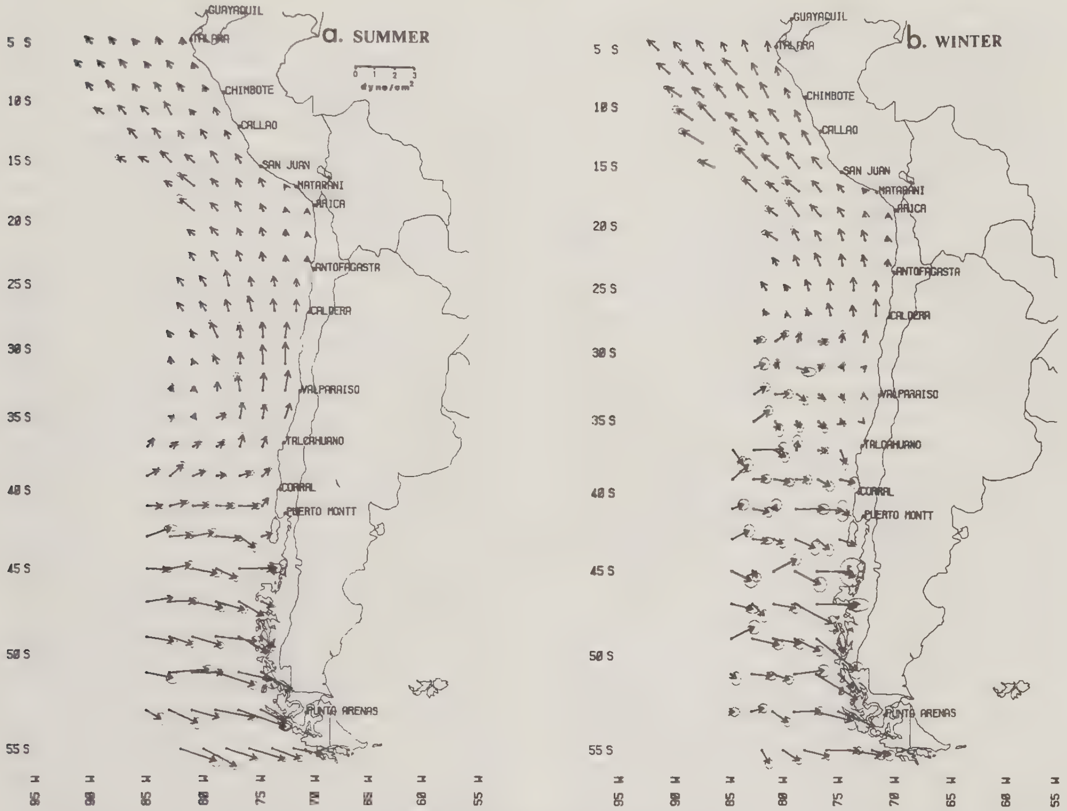

Figure 5. Wind stress on the sea surface (dynes cm^{-2}). Magnitude is indicated by length of symbol (see scale on figure); direction is indicated by orientation of symbol. Standard errors of the means of the meridional and zonal components are indicated by the vertical and horizontal axes of the elipses plotted at the head of each symbol. Computation of stress is as described by Bakun et al. 1974. *(a)* Summer (Nov., Dec., Jan., Feb.). *(b)* Winter (May, June, July, Aug.).

Chilean stock are in the vicinity of the fishery at Talcahuano (36°S).

Meristic, morphometric, electrophoretic, and tagging studies with *E. mordax* suggest that there are at least three stocks in the California Current region (McHugh 1951; Vrooman et al. 1981; Haugen et al. 1969). According to Richardson (1980) the spawning grounds of the northern stock are centered at about 44°-46°N in the Columbia River plume; spawning occurs in summer, and is highly concentrated in July. The central stock's spawning grounds are principally in the Southern California Bight (30°-34°N); spawning occurs throughout the year, with a distinct maximum from February to April and a minimum from August to October (Lasker and Smith 1977). Both the Californian and Mexican anchovy fisheries are based on the central stock, which in recent years has been the largest of the three. The spawning grounds of the southern stock are centered in southern Baja California (25°-28°N); the peak spawning season is similar to that of the central stock, but slightly earlier in the year. Peak larval abundance occurs from January to March (Smith 1972).

The Peruvian anchoveta stock was by far the largest of the Engraulid stocks of the Peru and California Current regions, and it has supported fisheries at least one order of magnitude greater than any of the other stocks. Landings for the period just before its collapse averaged about 10 million metric tons (MT) per year (Valdivia 1980), and virtual population estimates show that the spawning biomass averaged about 20 MT during the early years of the fishery (Csirke 1980). It is difficult to determine the catches or population size of the Peru-Chilean stock, for it was a minor but undetermined proportion of the Peruvian landings and a major proportion of the Chilean land-

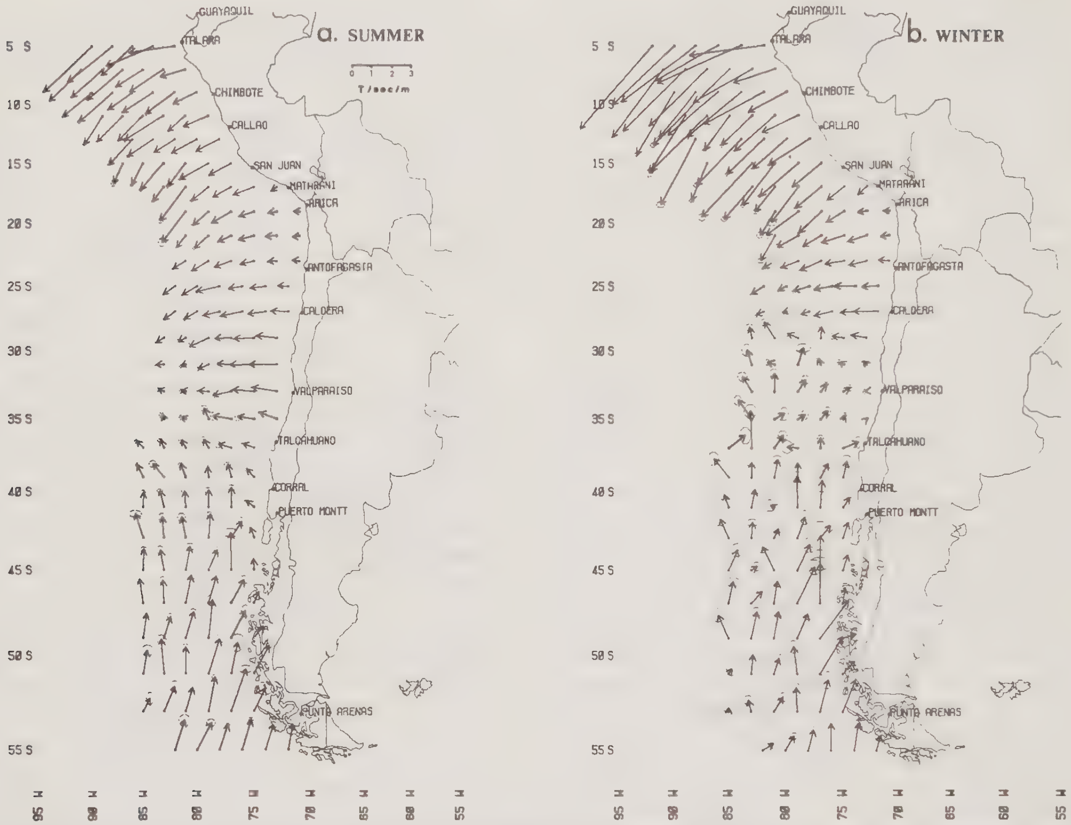
a. SUMMER
b. WINTER
0 1 2 3
T/sec/m
GUAYAQUIL
TALARA
CHIMBOTE
CALLAO
SAN JUAN
MATARANI
ARICA
ANTOFAGASTA
CALDERA
VALPARAISO
TALCAHUANO
CORRAL
PUERTO MONTT
PUNTA ARENAS
5 S
10 S
15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
55 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W
60 W
55 W

Figure 6. Surface Ekman transport (metric tons per second per meter) computed from the wind stress vectors shown in Figure 5. *(a)* Summer (Nov., Dec., Jan., Feb.). *(b)* Winter (May, June, July, Aug.).

ings. The peak Chilean landings of anchoveta were just under 1 MT (Boré and Martínez 1981), the great majority of which was apparently from the Peru-Chilean stock, since the landings from the Talcahuano region, which did not separate *Clupea* and *Engraulis,* had a maximum of just less than 0.2 MT.

The central stock is the only one of the three California Current stocks that has been extensively fished. Combined catches of the Mexican and Californian fisheries on this stock have recently reached 0.3 MT. Peak landings would have undoubtedly been larger than this if the California fishery had not commenced under intense regulation. Spawning biomass estimates based on larval surveys are available for the three California Current stocks. Estimates for the northern stock, based on two years of surveys and several different methods of calculating spawning biomass, vary between 0.14 MT and 1.0 MT (Richardson 1980). Larval surveys during the 1960s suggested that the spawning biomass of the central stock was from 3 to 4 MT, and the southern stock averaged about 1 MT (Vrooman and Smith 1972). Recent spawning biomass estimates based on egg surveys and Hunter and Goldberg's (1980) and Hunter and Macewicz's (1980) recent findings on the reproductive physiology of the northern anchovy suggest that the biomass estimates based on larval surveys were too large (Stauffer and Piquelle 1981).

The available evidence suggests that the virgin biomass of the Peruvian *Engraulis* stock was about 20 MT; the Peru-Chilean and Southern California Bight stocks were about 1-4 MT, with the Peru-Chilean stock probably the larger of the two. The stocks spawning near Talcahuano, in the Columbia River plume, and off of southern Baja California were both probably less than 0.5 MT.

Sardine

Radovich (1981) reviewed the available information on the sardine *Sardinops sagax* in the California Current region and concluded that there was good evidence for three stocks and sufficient evidence to hypothesize a fourth stock. Two of the stocks occurred together with the southern and central stocks of anchovy, respectively. The Gulf of California stock has no anchovy counterpart, and the hypothesized fourth stock would be a counterpart to the northern stock of anchovy. During the peak of the sardine fishery, landings varied from about 0.5 MT to 0.8 MT. Landings from the Southern California Bight were only 0.1 to 0.2 MT, with the rest coming from central California, which was the major fishing area, and from the Oregon to British Columbia region. Landings in central California and possibly those in the Oregon to British Columbia areas, were derived from sardines that used the upwelling region as feeding grounds and that migrated to the Southern California Bight for spawning.

The fishery for the sardine *Sardinops sagax* in the Peru Current system is quite recent, and therefore there is little published information on the population structure. The information presented below is primarily from Santander (1981) in the case of Peru and from the Chilean Fisheries Resource Catalogue (Boré and Martínez 1981) in the case of Chile. In Peru the area in which eggs and larvae of sardine were found has expanded considerably since 1972, when eggs were largely limited to northern Peru and were primarily located farther offshore than the anchoveta eggs and larvae. Since 1972 the co-occurence of anchoveta and sardine eggs and larvae has increased, and sardine eggs and larvae are common all along the Peruvian coast; however, the area of most intense spawning is still in northern Peru (i.e., 5°-11°S). In Chile there is extensive spawning in the area between Arica and Antofagasta (18°-23°S), and eggs have been found as far south as Isla Mocha (38°S. B.J.R. Serra, pers. comm.). The fishery is the most intense in the Arica to Coquimbo area (18°-30°S); however, since 1978 there have been substantial catches in the Talcahuano area (37°S). Chilean sardine landings reached 1.6 MT in 1979.

TRANSPORT, TURBULENCE, AND REPRODUCTION

The same data used to produce the 4-month seasonal distributions (Figures 4, 5, 6) were subdivided into 2-month sets in order to plot the seasonal progression of turbulent mixing and offshore transport conditions (Figure 7) and of turbulence and alongshore stress conditions (Figure 8) for the spawning centers and other significant areas. Characteristic 2-month values of the cube of wind speed for selected locations in the California Current region were assembled from the distributions presented by Husby and Nelson (this volume); corresponding estimates of alongshore stress and offshore Ekman transport were assembled from Nelson's (1977) charts.

The area off Chimbote, which is the spawning center of the major anchoveta stock, is low in average wind-generated turbulence throughout the year. However, offshore Ekman transport is large (Figure 7), particularly during the winter, when it is the maximum plotted for all areas. Because of Chimbote's proximity to the equator it is possible that Ekman transport overestimates the actual transport; when plotted in terms of alongshore stress (Figure 8), which avoids addressing the effect of rapid decrease of Coriolis near the equator, the cycle at Chimbote shifts toward the origin. One might hypothesize that the spawning of anchoveta during the season of largest alongshore stress (offshore transport) may be related to avoidance of detrimental effects of intermittent El Niño events, which occur most intensely during the Southern Hemisphere summer.

The seasonal pattern in the Southern California Bight, which is the principal spawning ground for the pelagic fishes of the California Current, including the central subpopulation of northern anchovy, is near the origin in both diagrams (Figures 7 and 8). However, it may be noted that the lowest average turbulence is encountered in the summer and fall, whereas spawning is most common in the spring and also in the winter in the case of anchovy. One may hypothesize that the relationship to the upwelling cycle may be the factor that determines spawning seasonality given the low turbulence and offshore transport conditions within the bight throughout the year.

The area off Arica near 18°S is consistently very low in both wind-generated turbulence and offshore transport. This area resembles the Southern California Bight in this and in several other respects, including warm coastal temperature anomalies during summer and location directly downstream from maximum upwelling regions. We need more information about the extent of spawning to properly evaluate its comparative significance.

In comparison to the three largest anchovy stocks of the eastern Pacific, the three smaller stocks appear to spawn in regions of somewhat higher turbulence. The southern Baja California stock spawns in an area where turbulence and offshore transport are moderate throughout the year, with values somewhat higher in the winter-spring transition than during the rest of the year. The high-latitude stocks (the northern stock of

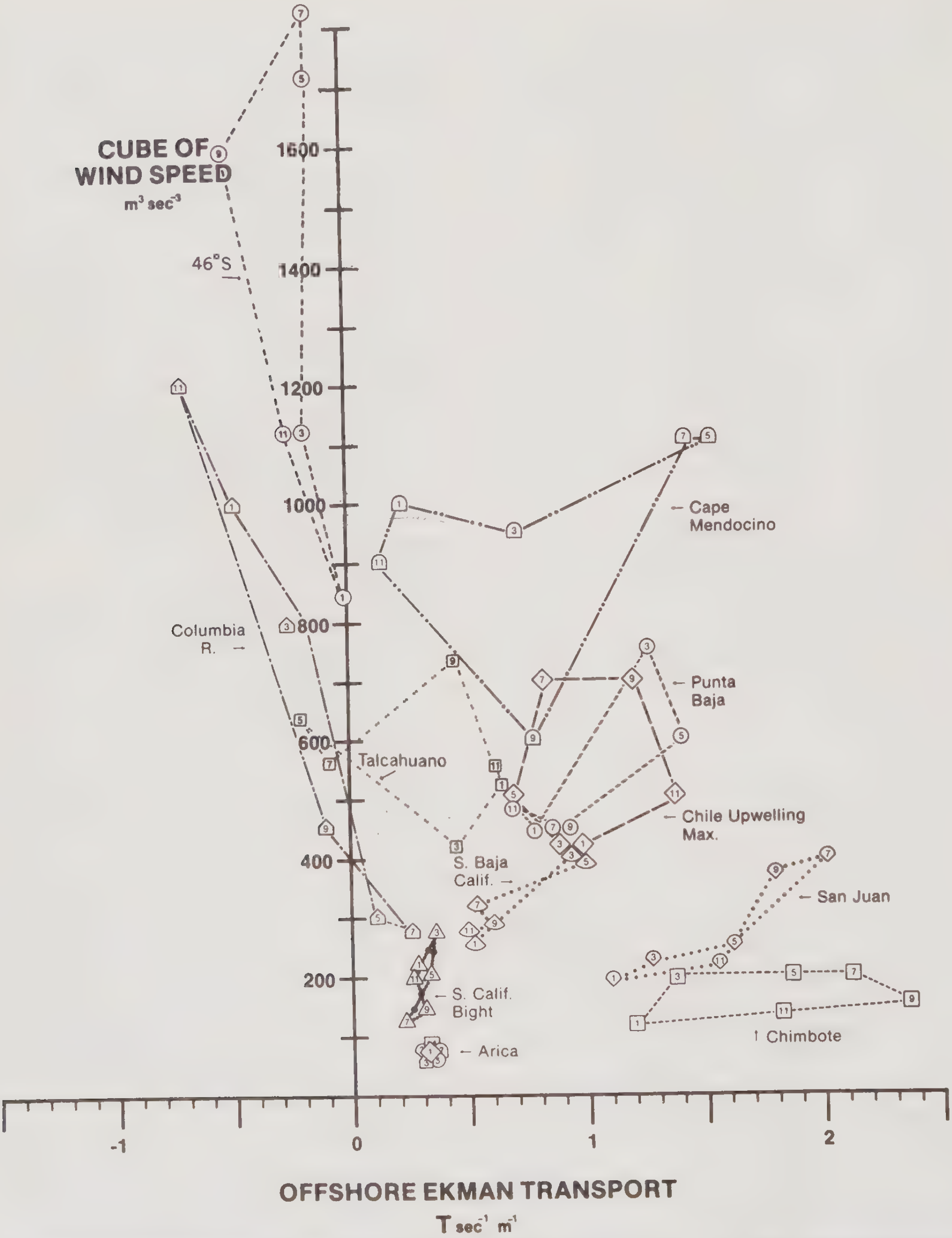

Figure 7. Characteristic seasonal relationships of turbulent mixing energy production (proportional to cube of wind speed) and offshore-directed Ekman transport for various locations off the west coasts of North and South America. Each numbered symbol represents a 2-month sample, with the number corresponding to the first month of the two (e.g., 1 represents Jan.-Feb., 3 represents Mar.-Apr., etc.).

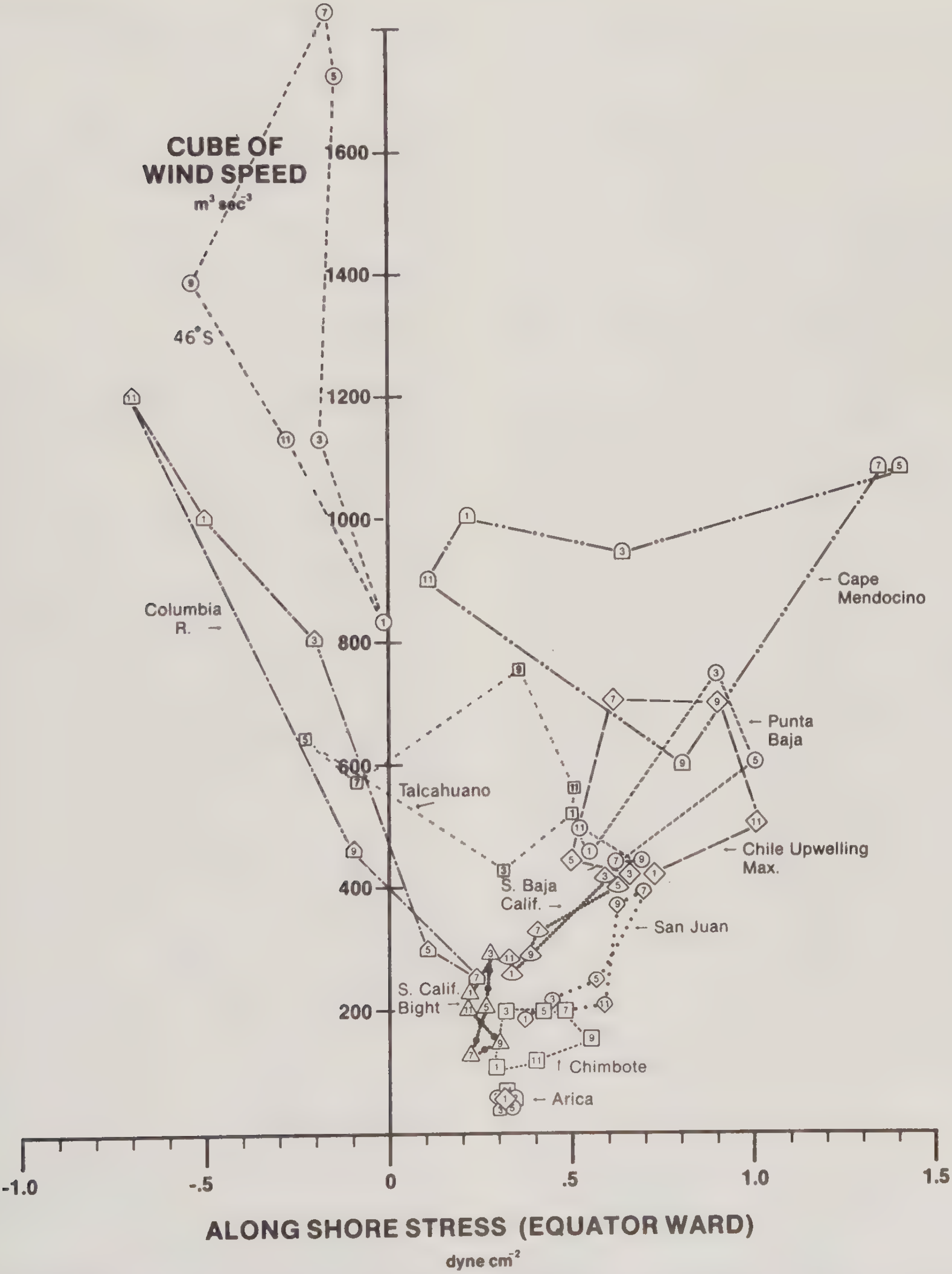

Figure 8. Characteristic seasonal relationships of turbulent mixing energy production (proportional to cube of wind speed) and alongshore wind stress (positive equatorward) for various locations off the west coasts of North and South America. Each numbered symbol represents a 2-month sample, with the number corresponding to the first month of the two (e.g., 1 represents Jan.-Feb., 3 represents Mar.-Apr., etc.).

anchovy, which spawns in the Columbia River plume, and the Talcahuano anchoveta stock) spawn in areas where turbulence is considerably higher than in the other spawning centers and where Ekman transport varies seasonally from onshore to offshore. The stock spawning in the Columbia River plume does so only in the summer, when the seasonal progression enters the space in the diagrams where the other stocks spawn. The Talcahuano stock (if it is a separate stock) is reported as spawning mainly in embayments protected from the higher levels of turbulence occurring off the coast (F.L.E. Robles, pers. comm.).

In the diagrams, the space occupied by the upwelling centers within the regions of maximum upwelling tends to be displaced toward the upper right of the space occupied by the spawning areas: e.g., Cape Mendocino (39°N), San Juan (15°S), and the Chilean upwelling maximum (30°S). This is also the case for the Punta Baja (30°N) area, which is a secondary upwelling region. The seasonal progression at 46°S latitude has a similar shape and orientation to that off the Columbia River at 46°N but is situated at a substantially higher turbulence level, never entering the areas in the diagrams occupied by the spawning regions. We would therefore not expect an extreme southern stock to be able to reproduce successfully enough to maintain a significant population at this latitude in the South American system.

In this connection, it is recognized that the meteorological and oceanographic ‘‘equators’’ are located to the north of the geographical equator, and thus a strict correspondence in latitude might not be expected; i.e., analogous features might be closer to the equator in the Southern Hemisphere than in the Northern Hemisphere. However, note that very much the same space is occupied in the diagrams by the Chilean upwelling maximum at 30°S and by the upwelling center at Punta Baja at 30°N; even the march through the annual cycle is in the same sense, although of course 6 months out of phase.

In concluding our discussion of the diagrams (Figures 7 and 8), we must comment on the precision of the displayed estimates. Available marine surface data are particularly sparse in certain coastal regions off South America, so sampling variability is a problem. Also, gradients in real distributions occur on small scales, which are not well resolved by our summaries. Thus, while we are confident in the general relationships of the spaces displayed, certain smaller details are less certain. For example, the indication of stronger offshore transport off Chimbote during September-October than during July-August may not be reliable; note that because of Chimbote's proximity to the equator the horizontal axis of its seasonal pattern in the transport diagram (Figure 7) is greatly expanded relative to that in the stress diagram (Figure 8).

CONCLUDING REMARKS

This paper represents only a ‘‘first cut’’ through the information available in the collected marine observations and accumulated knowledge of spawning habits. We are convinced that comparative studies are (1) useful for understanding linkages between fish stocks and environmental processes that are often extremely difficult to investigate experimentally, and (2) very cost-effective when making use of data for which the investment has already been made.

Figures 7 and 8 represent two potential dimensions of a multivariate ‘‘reproductive habitat space.’’ To the extent that the other crucial dimensions can be isolated and the favorable intervals defined, the excursions by various spawning sites into and out of the favorable space can perhaps be monitored, providing a basis for formulating empirical models that could be used to predict and simulate effects of management actions.

In adopting this view it is important to recognize the differences in scale, both of time and space, on which the various environmental processes affect eventual recruitment. For example, the critical time scale for turbulence to induce mortality by dissipating food concentrations may be several days at most. The effects of transport of larvae are expected to act on scales of a month or more, with consequences extending into the juvenile stage. Upwelling variations on seasonal and interannual time scales may affect the average background concentration of food organisms, which underlies the patterns altered by the short-scale turbulence mechanism. Likewise, upwelling and its associated offshore transport may be a favorable factor on long time scales and broad space scales, i.e. previous to the spawning season and upstream of spawning grounds, and an unfavorable factor when acting at the precise time and location that larvae may be present. We have noted a pattern of avoidance of upwelling maximum regions and areas of high turbulence in the spawning strategy of engraulids. An exception is the situation off north-central Peru, where an enormous engraulid population has existed in what we are calling an upwelling maximum region. In this case the steadiness of the upwelling process and the low turbulent mixing, which is unique to this region, could be a factor. Smaller-scale upwelling centers, e.g., the area near San Juan, which exist within the larger-scale upwelling maximum region, appear to be avoided in spawning habits (Santander 1981).

One preliminary comparative result with direct management implications is worth noting. The recent alternations between anchovy domination and sardine-mackerel domination in the two systems have yielded the consistent experience that the exploitable biomass in a sardine- and mackerel-dominated system is located poleward compared to that in an anchovy-dominated system. Thus the shifts in species composition have resulted in a spatial shift of the patterns of exploitation across national boundaries, where they appear to have a tendency to remain. The possibility of shifting the exploitable component of the organic production of a shared system to another nation's waters presents a particularly strong argument to a self-interested nation against overexploitation of the resources off its own coast.

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NORTHERN ANCHOVY AND PACIFIC SARDINE SPAWNING OFF SOUTHERN CALIFORNIA DURING 1978-80: PRELIMINARY OBSERVATIONS ON THE IMPORTANCE OF THE NEARSHORE COASTAL REGION

GARY D. BREWER
Institute for Marine and Coastal Studies
University of Southern California
University Park
Los Angeles, California 90007

PAUL E. SMITH
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Estimates of egg and larval abundance of northern anchovy *(Engraulis mordax)* and larval abundance of Pacific sardine *(Sardinops sagax caeruleus)* from monthly Ichthyoplankton Coastal and Harbor Studies (ICHS) cruises during 1978-80 within the nearshore Southern California Bight (to the 43-m isobath) were contrasted with comparable estimates from CalCOFI region 7. The ICHS region encompassed 3.8 percent of the area in region 7.

Raw survey data, uncorrected for potential sampler biases, indicated that about 3 percent of northern anchovy larvae occurred within the nearshore zone relative to the entire region 7. This number may be equivalent to about 2 percent of the larvae spawned by the central subpopulation.

The abundance of Pacific sardine larvae in the coastal region increased from 1978-79 to 1979-80. Sardine larvae occurred most frequently during the summer and fall and were captured most often in Santa Monica Bay. CalCOFI data on Pacific sardine were too infrequent for comparison with ICHS data.

The ichthyoplankton data sets are discussed in relation to the nursery function of nearshore versus offshore waters and the need for additional criteria for assessing recruitment potential from the two regions.

RESUMEN

Se comparó la abundancia estimada de huevecillos y larvas de la anchoveta *Engraulis mordax* y la abundancia de larvas de la sardina del Pacífico *(Sardinops sagax caeruleus)*, determinadas en los cruceros mensuales de Estudios del Ictioplancton en Puertos y la Costa (ICHS) durante 1978-80 en la zona costera del sur de California (hasta la isóbata de los 43 m.), con estimaciones comparables de la región 7 de CalCOFI. La región del ICHS abarcaba un 3.8 por ciento del área en la región 7.

Los datos sin procesar y sin corrección de los sesgos potenciales del muestreador mostraban que alrededor del 3 por ciento de las larvas de anchoveta ocurrieron en la zona cercana a la costa por toda la región 7. Este número podría ser equivalente a alrededor del 2 por ciento de las larvas producidas por la subpoblación central.

La abundancia de la sardina del Pacífico en la región costera aumentó de 1978-79 a 1979-80. Las larvas de sardina se observaron con mayor frecuencia durante el verano y otoño y se capturaron más a menudo en la Bahía de Santa Mónica. Los datos de CalCOFI referentes a la sardina del Pacífico eran muy poco frecuentes como para compararlos con los datos del ICHS.

Los datos del ictioplancton son discutidos en relación a la función de criaderos en las aguas cercanas a la costa contra aquéllos fuera de la costa, así como la necesidad de criterios adicionales para evaluar el potencial de reclutamiento de las dos regiones.

INTRODUCTION

The variable abundance and distribution of the early life stages of clupeiform fishes off the Pacific coast of North America have been investigated for more than three decades by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) (Ahlstrom 1966; Smith 1972). The time series on ichthyoplankton, developed by CalCOFI, was supplemented from 1978-80 by a regionally intensive project within the Southern California Bight; the project was entitled Ichthyoplankton Coastal and Harbor Studies (ICHS).

The ICHS data includes temporal and spatial features of ichthyoplankton abundance that are not available from CalCOFI cruises. Important differences exist in the species structure of ichthyoplankton between ICHS and adjacent CalCOFI regions (Brewer et al. 1980; Loeb et al.[1]). Other investigators have shown gradients in potential food for larval fishes—phytoplankton (Eppley et al. 1978; Kleppel 1980) and microzooplankton (Beers and Stewart 1967; Arthur 1977)—that increase toward shore. The ICHS data make it possible to assess longshore variability of ichthyoplankton within the bight and, with CalCOFI data, to evaluate nearshore versus offshore regions as spawning grounds for adult fishes and as habitats for the survival of larvae.

[Manuscript received February 8, 1982.]

[1] Loeb, V., H. Moser, and P. Smith. Seasonal and geographic patterns of ichthyoplankton distributions in the CalCOFI area, 1975. Admin. Rep., unpub.

This report gives estimates of egg and larval abundance of northern anchovy *(Engraulis mordax)* and larval abundance of Pacific sardine *(Sardinops sagax caeruleus)* from monthly cruises within the nearshore ICHS region. These estimates are compared with similar estimates from an adjacent CalCOFI region. The data sets are discussed in relation to the nursery function of nearshore versus offshore waters and the need for additional criteria for assessing recruitment potential from the two regions.

ICHS sampled the nearshore Southern California Bight along the 8-m, 15-m, 22-m, and 36-m isobaths, inshore of most CalCOFI stations. The circulation and chemistry of these shallow waters are not well studied (Jones 1971; Tsuchiya 1980; Winant and Bratkovich 1981). Compared to offshore waters, coastal features are complicated by boundary effects, shoreline topography, local wind conditions, runoff from sporadic rainfall, and anthropogenic influences. Industrial, municipal, and thermal wastewaters from at least 24 discrete outfalls are discharged within the Southern California Bight (Southern California Coastal Water Research Project 1973).

MATERIALS AND METHODS

Sampling techniques and laboratory procedures used by the CalCOFI program have been discussed in detail by Kramer et al. (1972) and Smith and Richardson (1977). Briefly, 70-cm bongo[2] plankton samplers (0.505-mm mesh) were lowered to 210 m, depth permitting, and retrieved at 20-m•min^{-1} while a constant towing wire angle was maintained. Plankton samples were preserved and returned to the laboratory, where they were sorted and the fish eggs and larvae identified and enumerated. Data on tow depth, volume of water filtered, and numbers of eggs and larvae in each sample were then used to estimate ichthyoplankton abundance under unit areas of sea surface.

An important goal of the ICHS program was data compatibility with CalCOFI. Hence, a primary objective in the nearshore sampling (as in CalCOFI surveys) was an oblique tow trajectory with 70-cm bongos, whereby equal volumes of water were filtered per unit depth. Certain details of the ICHS methodology differed from CalCOFI techniques. ICHS sampled almost exclusively at night, whereas CalCOFI sampled during all hours. The ICHS bongo was fitted with a messenger release, opening-closing device as described by McGowan and Brown (1966). A steel bar, 0.7 m long and weighing about 40 kg, was tied 0.3 m below the bongo frame as a depressor weight. The nets were made of 0.333-mm mesh Nitex with a 1.5-m cylindrical section and a 1.5-m conical section leading to 0.333-mm mesh cod-end sock.

The ICHS bongo was slowly lowered to the bottom (canvas doors covered the mouths of the nets) with the ship under way. The angle and length of the towing wire were monitored in order to bump the depressor weight on the bottom. The canvas doors were then opened by messenger and the sampler retrieved immediately at a constant rate of 20-m•min^{-1} while maintaining a towing-wire angle of about 45°. A General Oceanics instrumented trawl block provided continuous readings of towing-wire angle, meters of cable out, and retrieval rate. Ship speed was monitored by a General Oceanics speedometer with a deck readout. General Oceanics flowmeters, located in the mouth of the bongo frame, were used to compute the distance traveled by the nets; from this data, the volume of water filtered was determined. With a combined ship speed and net retrieval rate of about 1.0-1.1-m•sec^{-1}, about 3-4 m^3 of water were filtered per meter of depth.

A depth transducer was mounted on the bongo frame beginning with cruise 12 to insure contact with the bottom by providing continuous depth readings of the sampler via a deck readout.

Fish eggs and larvae were carefully sorted from 25-100 percent of each sample with the aid of stereomicroscopes. Aliquots were made by using either the port or starboard bongo sample, and/or by splitting with a Folsom plankton splitter (McEwen et al. 1954). Ten percent of each sorted fraction was checked to ensure that sorting efficiency remained at least 90 percent. Fragmented larvae were counted, but were not considered in the determination of sorting efficiency prior to July 1979. Also, some samples collected prior to July 1979 were not sort-checked. Data for these cruises may underestimate abundance relative to subsequent cruises, but probably by no more than 5 percent, based on the numbers of fragments found and the sorting efficiency during the later cruises.

We have assumed that damaged specimens identified conservatively as engraulids and clupeids were, in fact, *Engraulis mordax* and *Sardinops sagax caeruleus*, respectively. Also, damaged specimens identified only as clupeiformes have been proportioned into the two specific categories for each sample, based on the ratio of individuals identified positively.

While the central subpopulation of northern anchovy encompasses at least eight CalCOFI regions and an area of about 571,000 km^2 (Vrooman et al. 1980), in this report data from region 7 only were compared with the ICHS data. The ICHS region is contiguous with region 7 (Figure 1), and region 7 is the center of

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[2] Cruise 7901 used the CalCOFI 1-m bridled net.

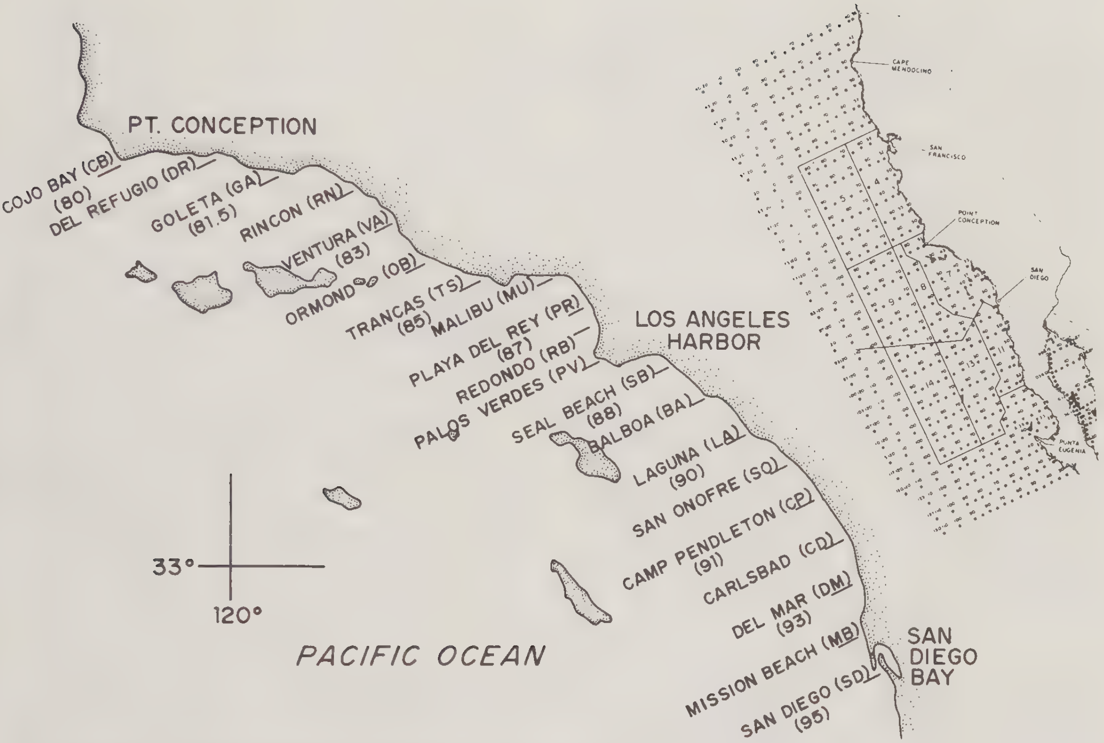
PT. CONCEPTION
COJO BAY (CB) (80)
DEL REFUGIO (DR)
GOLETA (GA) (81.5)
RINCON (RN)
VENTURA (VA) (83)
ORMOND (OB)
TRANCAS (TS) (85)
MALIBU (MU)
PLAYA DEL REY (PR) (87)
REDONDO (RB)
PALOS VERDES (PV)
LOS ANGELES HARBOR
SEAL BEACH (SB) (88)
BALBOA (BA)
LAGUNA (LA) (90)
SAN ONOFRE (SO)
CAMP PENDLETON (CP) (91)
CARLSBAD (CD)
DEL MAR (DM) (93)
MISSION BEACH (MB)
SAN DIEGO (SD) (95)
SAN DIEGO BAY
33°
120°
PACIFIC OCEAN
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

Figure 1. Locations of ICHS transects in relation to adjacent CalCOFI regions (inset). The ICHS region includes the area from shore to the 43-m isobath—approximately 3.8 percent of the area within region 7.

the northern anchovy central subpopulation biomass (Smith and Eppley 1981).

Station locations for ICHS and CalCOFI region 7 are listed in Tables 1 and 2, respectively. Stations occupied by ICHS varied between June 1978-July 1979 (Phase I) and August 1979-July 1980 (Phase II). Phase I sampling encompassed 10 transects and 4 stations per transect over isobaths of 8, 15, 22, and 36 m (Table 1). Data from eight ICHS cruises were available from this period. Phase II cruises occupied 46 stations each month along 20 transects. Only the 8-m and 22-m isobaths were sampled along 17 of the transects. Transects off Ormond, Redondo, and San Onofre beaches were sampled at 8-m, 15-m, 22-m, and 36-m isobaths. The volume of water filtered per unit depth was increased by a factor of four during Phase II, relative to Phase I. This was accomplished by decreasing the net retrieval rate from 20-m•min^{-1} to 10-m•min^{-1} and replicating each sample. The speed of the net (i.e., retrieval rate + ship speed) was maintained at about 1.0-1.1 m•sec^{-1} during both Phase I and II.

For purposes of this report, the ICHS stations represent a nearshore region that extends from just below the United States-Mexico border (32°24.5'N) to just above Pt. Conception (34°40.0'N). and extends offshore to the 43-m isobath (Figure 1). This area encompasses about 2652 km^2 that lie within the area (69,055 km^2) of CalCOFI region 7. The area of the ICHS region was determined by multiplying the longshore distance covered by the transects as determined from National Ocean Survey charts 19720 and 18740. The distance to the 43-m isobath was estimated by extrapolating the average seaward distance of the ICHS stations along the 8-m, 15-m, 22-m, and 36-m isobaths.

Station data from both CalCOFI and ICHS regions were scaled for each taxon to numbers of individuals under unit areas of sea surface (Smith and Richardson 1977). Regional census estimates (Smith 1972) for each survey cruise were computed from the mean number of eggs or larvae per m^2 of sea surface for all stations sampled, times the area within the respective region.

TABLE 1
ICHS Station Coordinates

Transect	Station (depth-m)	N. Latitude	W. Longitude	Distance from shore (km)
80				
(Cojo Bay)	* 08	34°26.8′	120°26.7′	0.35
	15	34°26.7′	120°26.5′	0.79
	* 22	34°26.5′	120°26.5′	1.17
	36	34°26.2′	120°26.5′	1.20
DR				
(Del Refugio)	* 08	34°27.5′	120°03.0′	0.20
	* 22	34°27.3′	120°04.4′	0.31
81.5				
(Goleta)	* 08	34°24.6′	119°47.4′	0.74
	15	34°24.1′	119°46.4′	1.00
	* 22	34°23.9′	119°46.5′	1.33
	36	34°23.5′	119°46.5′	2.04
RN				
(Rincon)	* 08	34°22.0′	119°27.5′	0.25
	* 22	34°21.4′	119°28.7′	1.40
83				
(Ventura)	* 08	34°15.7′	119°16.6′	0.35
	15	34°14.9′	119°17.3′	1.79
	* 22	34°13.4′	119°21.5′	7.50
	36	34°11.9′	119°24.1′	11.95
OB				
(Ormond Beach)	* 08	34°07.3′	119°10.4′	0.28
	* 15	34°07.1′	119°10.9′	0.79
	* 22	34°06.6′	119°11.8′	1.70
	* 36	34°06.1′	119°12.8′	2.55
85				
(Trancas)	* 08	34°03.1′	118°58.2′	0.37
	15	34°02.8′	118°58.0′	0.94
	* 22	34°02.6′	118°58.0′	1.26
	36	34°02.2′	118°58.0′	1.67
MU				
(Malibu)	* 08	34°02.2′	118°36.2′	0.11
	* 22	34°01.6′	118°37.4′	0.56
87				
(Playa del Rey)	* 08	33°57.0′	118°27.2′	0.41
	15	33°57.0′	118°27.9′	1.48
	* 22	33°57.0′	118°28.6′	2.41
	36	33°57.0′	118°30.1′	4.43
RB				
(Redondo Beach)	* 08	33°50.3′	118°23.7′	0.20
	* 15	33°50.1′	118°23.8′	0.50
	* 22	33°50.0′	118°24.2′	0.82
	* 36	33°49.6′	118°24.9′	1.57
PV				
(Palos Verdes)	* 15	33°40.7′	118°24.7′	0.19
	* 22	33°44.4′	118°25.0′	0.39
88				
(Seal Beach)	* 08	33°42.4	118°04.4′	0.93
	15	33°41.1	118°04.6′	3.52
	* 22	33°39.4′	118°05.0′	5.30
	36	33°37.2′	118°05.4′	8.37
BA				
(Balboa)	* 08	33°36.2′	117°54.5′	0.21
	* 22	33°35.9′	117°54.9′	0.62
90				
(Laguna Beach)	* 15	33°30.3′	117°45.3′	0.52
	22	33°30.3′	117°45.5′	0.74
	* 36	33°30.2′	117°45.8′	1.24
SO				
(San Onofre)	* 08	33°21.7′	117°33.8′	0.50
	* 15	33°21.2′	117°34.6′	1.45
	* 22	33°20.7′	117°35.3′	2.01
	* 36	33°20.6′	117°35.8′	2.54
91				
(Camp Pendleton)	* 08	33°15.1′	117°26.4′	0.70
	15	33°14.6′	117°27.2′	2.31
	* 22	33°14.3′	117°27.5′	3.26
	36	33°13.7′	117°28.2′	4.39
CD				
(Carlsbad)	* 08	33°07.4′	117°20.2′	0.27
	* 22	33°07.1′	117°20.7′	0.72
93				
(Del Mar)	* 08	32°57.6′	117°16.3′	0.52
	15	32°57.6′	117°16.7′	1.04
	* 22	32°57.5′	117°17.1′	1.63
	36	32°57.5′	117°17.5′	2.22
MB				
(Mission Beach)	* 08	32°46.7′	117°15.4′	0.25
	* 22	32°46.3′	117°16.5′	1.13
95				
(San Diego)	* 08	32°37.9′	117°08.7′	0.44
	15	32°37.8′	117°09.8′	2.00
	* 22	32°36.9′	117°11.3′	4.89
	36	32°35.8′	117°13.6′	9.07

Stations along numerically designated (CalCOFI) transects 80-95 were sampled from June 1978-July 1979 (Phase I). Stations marked by an "*" were sampled from August 1979-July 1980 (Phase II). Note that no samples were collected at the 8-m isobath along transects PV and 90.

TABLE 2
CalCOFI Region 7 Station Coordinates

Transect	Station	(Depth-m)	N. Latitude	W. Longitude	Distance from shore (km)*
80	51.0	110	34°27.0′	120°31.4′	4.6
	52.0	242	34°25.0′	120°35.6′	11.9
	55.0	763	34°19.0′	120°48.1′	30.9
	60.0	2151	34°09.0′	121°09.0′	66.5
82	46.0	539	34°16.2′	119°56.3′	16.1
	47.0	541	34°14.2′	120°00.5′	22.8
83	40.6	33	34°13.5′	119°24.7′	10.2
(83.3)	42.0	167	34°10.7′	119°30.5′	19.1
	51.0	213	33°52.7′	120°08.0′	63.5
	52.0	410	33°50.7′	120°12.1′	69.3
	55.0	981	33°44.7′	120°24.6′	77.8
87	32.5	24	33°54.4′	118°27.3′	2.8
(86.7)	32.7	33	33°54.0′	118°28.2′	4.3
	33.0	49	33°53.4′	118°29.4′	6.7
	34.0	70	33°51.4′	118°33.6′	14.1
	35.0	575	33°49.4′	118°37.7′	19.8
	36.0	801	33°47.4′	118°41.9′	24.8
	40.0	840	33°39.4′	118°58.5′	41.7
	45.0	1630	33°29.4′	119°19.1′	70.6
	50.0	77	33°19.4′	119°39.8′	99.6
	51.0	104	33°17.4′	119°43.9′	107.0
	55.0	1205	33°09.4′	120°00.4′	131.9
90	27.6	43	33°29.9′	117°44.4′	1.3
	28.0	302	33°29.1′	117°46.1′	2.8
	29.0	609	33°27.1′	117°50.2′	10.0
	30.0	616	33°25.1′	117°54.3′	17.2
	31.0	395	33°23.1′	117°58.5′	23.7
	33.0	751	33°19.1′	118°06.7′	36.5
	37.0	1173	33°11.1′	118°23.2′	58.9
	41.5	1372	33°02.1′	118°41.7′	84.1
	45.0	1720	32°55.1′	118°56.1′	103.7
	53.0	1138	32°39.1′	119°28.9′	157.4
93	26.7	45	32°57.4′	117°18.3′	3.5
	26.9	75	32°57.0′	117°19.1′	5.0
	28.0	553	32°54.8′	117°23.7′	10.9
	29.0	592	32°52.8′	117°27.8′	17.4
	30.0	779	32°50.8′	117°31.9′	23.3
	35.0	605	32°40.8′	117°52.4′	57.6
	40.0	1686	32°30.8′	118°12.8′	92.0
	45.0	1347	32°20.8′	118°33.3′	127.0
	50.0	1413	32°10.8′	118°53.6′	163.5
97	29.0	41	32°17.4′	117°04.8′	3.0
	30.0	59	32°15.4′	117°08.8′	10.6
	32.0	1289	32°11.4′	117°17.0′	25.0
	35.0	1183	32°05.4′	117°29.2′	47.6
	40.0	1489	31°55.4′	117°49.5′	84.6

*Nearest point on mainland.

RESULTS

Northern Anchovy Larvae

Northern anchovy spawn all year within the bight, but their estimated regional abundance may vary by a factor of 10 between adjacent months and a factor of 100 between adjacent seasons (Table 3). About 80 percent of northern anchovy spawning takes place in winter and spring (Stauffer and Parker 1980). CalCOFI sampling was concentrated during the months when anchovy spawning is greatest; ICHS sampled throughout the year. Seasonal spawning, possible biases resulting from different egg and larvae retention between the ICHS (0.333-mm mesh) net and the CalCOFI (0.505-mm mesh) net, and day-night differences in net avoidance require cautious comparison of ICHS and CalCOFI data.

The nearshore Southern California Bight contained an average of 38 *E. mordax* larvae per m^2 of sea surface during 1978-80 based on 861 plankton tows (Table 3). Similarly, during the same period, CalCOFI nets towed within region 7 captured an average of 102 larvae per m^2 from 466 plankton samples (Table 4). In order to eliminate temporal bias in comparing ICHS and CalCOFI regional abundance, nine surveys conducted during concurrent periods were contrasted (Tables 3 and 4). The relationship (Figure 2) between monthly census estimates of larval abundance in region 7 versus the ICHS region suggests that numbers of larvae covaried between the two regions. The overall means of the nine paired cruises were 5673 x 10^9 (82.4•m^{-2}) and 162 x 10^9 (61.1•m^{-2}) larvae in the two regions, respectively. The ICHS region, encompassing 3.8 percent of the area in region 7, contained about 3 percent of the northern anchovy larvae.

The abundance of larvae per m^2 varied directly with station depth within the ICHS region (Figure 3). This relationship indicates that the census data underestimated total numbers of larvae to the 43-m isobath during Phase II when stations over the 15-m and 36-m isobaths were not well represented (Table 1). Without data from the 15-m and 36-m isobaths, monthly census estimates were low by a factor of about 1.5 based on the regression equation in Figure 3. Figure 3 also shows that the average density of larvae (number per unit volume) rises to a near asymptote at the 36-m

TABLE 3
Summary of Egg and Larval Abundance of Northern Anchovy and Larval Abundance of Pacific Sardine from ICHS Cruises during 1978-80

		Engraulis larvae				*Engraulis* eggs				*Sardinops* larvae			
Cruise	Dates	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	Est. # larvae ICHS region (x 10^9)	# Sta./ positive	$\bar{x}$ eggs •m^{-2}	Std. dev.	Est. # eggs ICHS region (x 10^9)	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	Est. # larvae ICHS region (x 10^9)
	1978												
1*	12-24 Jun.	38/36	24.47	38.93	64.89	38/16	9.18	41.78	24.35	38/06	0.10	0.33	0.27
2*	10-21 Jul.	37/33	8.78	13.52	23.27	37/20	21.27	76.31	56.41	37/03	0.06	0.25	0.16
3	14-25 Aug.												
4	18-29 Sep.	39/35	12.76	18.93	33.85	39/18	11.67	44.27	30.95	39/03	0.04	0.13	0.10
5	16-27 Oct.	39/33	16.98	36.73	45.03	39/22	492.25	2878.47	1305.40	39/04	0.04	0.14	0.11
6	06-17 Nov.												
7	04-15 Dec.	39/36	32.18	45.64	85.33	39/27	14.69	54.12	38.96	39/01	0.01	0.09	0.04
	1979												
8*	08-19 Jan.	39/39	27.54	27.10	73.05	39/25	8.04	20.08	21.32	39/04	0.05	0.14	0.12
9	12-28 Feb.												
10*	12-23 Mar.	39/38	75.49	104.98	200.19	30/35	172.96	333.73	458.69	39/07	0.18	0.56	0.47
11*	02-21 Apr.	39/38	55.15	65.95	146.27	39/31	119.75	332.27	317.58	39/01	0.01	0.05	0.02
12	14-25 May												
13	11-22 Jun.												
14	10-18 Jul.												
15	13-24 Aug.	46/45	19.83	35.51	52.58	46/29	37.69	160.60	99.96	46/15	0.18	0.72	0.48
16	10-21 Sep.	46/46	15.05	27.60	39.90	46/24	2.61	6.90	6.93	46/21	0.31	0.66	0.83
17	08-18 Oct.	46/39	4.20	6.45	11.13	46/18	22.21	63.93	58.91	46/23	1.45	3.94	3.85
18	05-16 Nov.	46/25	2.73	9.66	7.25	46/25	15.11	46.76	40.07	46/12	0.18	0.44	0.49
19	03-13 Dec.	46/36	9.36	15.67	24.83	46/33	69.49	121.86	184.28	46/11	0.61	1.70	1.62
	1980												
20	07-19 Jan.	46/42	80.55	149.11	213.62	46/42	69.65	159.18	184.72	46/11	0.28	0.65	0.75
21*	11-28 Feb.	46/46	91.49	121.13	242.63	46/43	191.09	717.70	506.76	46/05	0.04	0.11	0.10
22*	10-22 Mar.	46/45	195.18	196.46	517.63	46/44	294.88	651.95	782.02	46/09	0.13	0.33	0.36
23*	07-17 Apr.	46/46	49.90	54.38	132.34	46/40	124.21	367.51	329.41	46/06	0.12	0.42	0.31
24*	12-25 May	46/43	22.17	38.47	58.79	46/33	33.92	117.21	89.96	46/10	1.93	11.43	5.11
25	16-26 Jun.	46/40	7.07	11.86	18.75	46/24	5.73	16.97	15.21	46/03	0.04	0.16	0.10
26	14-25 Jul.	46/30	1.63	2.24	4.31	46/15	4.26	23.54	11.29	46/00	0.00	0.00	0.00

*Cruises that were concurrent with CalCOFI cruises.

TABLE 4

Summary of Egg and Larval Abundance of Northern Anchovy and Larval Abundance of Pacific Sardine from CalCOFI Cruises during 1978-80

		Engraulis larvae				*Engraulis* eggs				*Sardinops* larvae			
Cruise	Dates	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	Est. # larvae region 7 (x 10^9)	# Sta./ positive	$\bar{x}$ eggs •m^{-2}	Std. dev.	Est. # eggs region 7 (x 10^9)	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	Est. # larvae region 7 (x 10^9)
	1978												
7801	05-24 Jan.	42/36	63.96	57.23	4,416.8	42/35	45.09	74.89	3,113.7	42/00	0.0	0.0	0.0
7803	18 Feb.-06 Mar.	42/42	267.81	356.41	18,493.6	42/36	79.99	133.41	5,523.7	42/02	0.071	0.39	4.9
7804	29 Mar.-14 Apr.	42/36	156.46	204.47	10,804.3	42/26	157.24	309.91	10,858.2	42/01	0.007	0.05	0.5
7805*	23 May-02 Jun.	34/29	42.74	134.14	2,951.4	34/13	10.96	36.21	756.8	34/01	0.029	0.17	2.0
7807*	20 Jun.-06 Jul.	41/18	6.75	8.64	466.1	41/08	1.47	5.89	101.5	41/02	0.039	0.17	2.7
7808	31 Jul.-16 Aug.	42/18	6.43	18.77	444.0	42/09	6.46	26.39	446.1	42/02	0.036	0.17	2.5
	1979												
7901*	15-22 Jan.	24/21	29.24	55.96	2,019.2	24/17	37.70	73.99	2,603.4	24/00	0.0	0.0	0.0
7902	19-28 Feb.	24/22	233.39	264.53	16,116.7	24/14	96.61	181.61	6,671.4	24/00	0.0	0.0	0.0
7903*	02-08 Mar.	27/25	117.38	144.40	8,105.7	27/17	44.80	80.31	3,093.7	27/00	0.0	0.0	0.0
7904*	06-17 Apr.	23/23	84.08	95.05	5,806.1	23/17	185.44	349.12	12,805.6	23/00	0.0	0.0	0.0
7905	30 Apr.-16 May	28/26	57.35	63.74	3,960.3	28/15	48.72	93.28	3,364.4	28/00	0.0	0.0	0.0
	1980												
8003a*	24 Feb.-02 Mar.	24/24	105.77	108.63	7,303.9								
8003b*	27 Mar.-06 Apr.	20/19	204.38	201.25	14,113.5								
8004*	11-29 Apr.	29/26	94.16	226.37	6,502.2		Data not available				Data not available		
8005*	24-30 May	24/17	56.75	117.63	3,918.9								

*Cruises that were concurrent with ICHS cruises.

isobath (2.2 larvae•m^{-3}). Extrapolation of a line fitted to the four X's in Figure 3 ($Y=2.63-14.07/X$) gives an average density estimate of 2.3•m^{-3} at the 43-m isobath (i.e., 99•m^{-2}). The asymptote suggests that the majority of anchovy occurred within the vertical depth range sampled by ICHS. Ahlstrom (1959) found that 85 percent of the anchovy larvae were distributed in the upper 48 m.

Larval abundance was not well correlated with distance from shore within the ICHS region (Figure 4), and no clear relationship was evident between the highest mean station abundance and distance from shore based on five complementary CalCOFI-ICHS transects (Figure 5). For example, along transect 80,

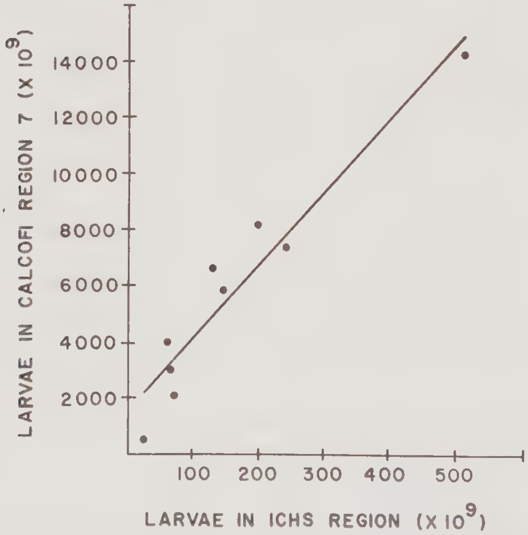

Figure 2. Monthly census estimates of northern anchovy larvae in the ICHS region versus CalCOFI region 7 ($Y=1530.0+25.65X$; $r^2=0.92$).

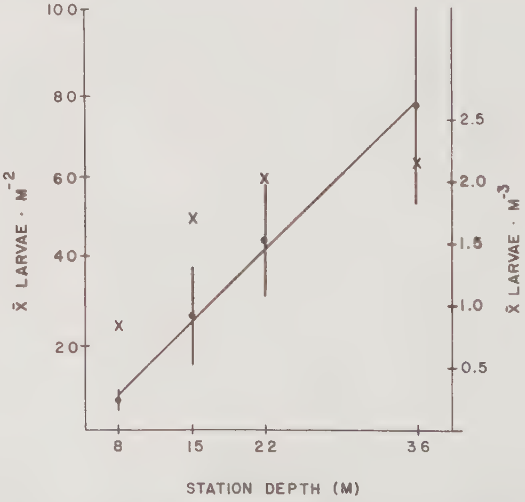

Figure 3. Average abundance per m^2 and 95 percent confidence intervals of northern anchovy larvae by station depth within the ICHS region ($Y=11.76+2.51X$). The points represent mean abundance by isobath from all Phase I transects and from those Phase II transects (three) where data from 8-m, 15-m, 22-m, and 36-m isobaths were collected ($N=453$). The X's represent equivalent data, expressed as mean abundance per m^3.

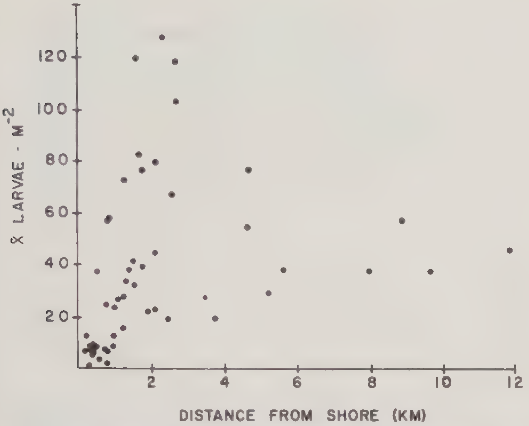

Figure 4. Mean station abundance of northern anchovy larvae by distance from shore. The points represent data from stations as described in Figure 3.

highest mean densities of larvae were found 1.2 km from shore; along transect 90, highest mean densities were found 103.6 km from shore. We have no explanation for the prominent dip in larval abundance that occurred along at least three of the five transects at distances between 10 and 20 km from shore.

We examined the variability of anchovy larvae in the longshore dimension by both average transect abundance and rank transect abundance (Tables 5 and 6). Table 5 summarizes all 1978-80 CalCOFI data along five transects and complementary data from nine CalCOFI-ICHS cruises. The within-transect averages between CalCOFI and ICHS are in surprisingly close agreement, while variability between transects is a factor of over 10 for CalCOFI transects and a factor of about 5 for ICHS transects. Because the standard deviations of the transect means were large, nonparametric techniques were used to test the signifi-

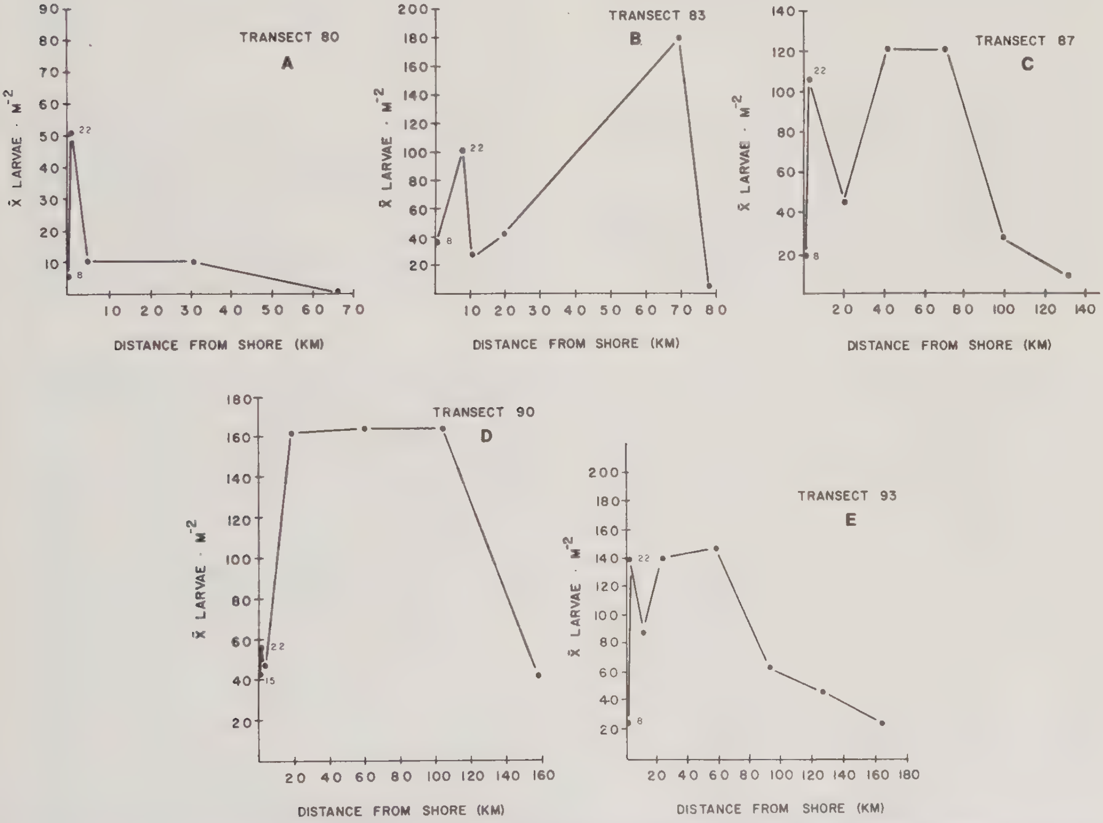

Figure 5. Average abundance of northern anchovy larvae along complementary CalCOFI-ICHS transects 80 *(A)*, 83 *(B)*, 87 *(C)*, 90 *(D)*, and 93 *(E)*. Mean station data were based on 9 concurrent CalCOFI-ICHS cruises (Tables 3 and 4) and only those CalCOFI and ICHS stations that were sampled during 1978, 1979, and 1980. ICHS stations are labeled.

TABLE 5

Abundance of Northern Anchovy Larvae along Complementary CalCOFI-ICHS Transects

	ICHS			CalCOFI					
	Nine concurrent cruises						All cruises 1978-1980		
Transect	# Sta./ positive	$\bar{x}$ larvae $\cdot m^{-2}$	Std. dev.	# Sta./ positive	$\bar{x}$ larvae $\cdot m^{-2}$	Std. dev.	# Sta./ positive	$\bar{x}$ larvae $\cdot m^{-2}$	Std. dev.
80	28/23	20.2	68.5	28/18	8.9	18.7	50/31	15.6	39.2
93	28/28	52.0	99.0	32/29	64.3	208.5	56/52	82.5	184.4
87	26/26	65.8	80.7	53/50	56.7	92.0	103/91	86.8	127.1
90	23/22	60.7	84.1	53/46	118.7	163.9	99/85	182.9	296.0
93	27/27	96.4	116.4	58/53	80.1	108.5	106/92	93.5	131.0

Concurrent cruises are designated in Tables 3 and 4.

TABLE 7

Transect Ranks of Northern Anchovy Egg and Larvae and Pacific Sardine Larval Abundance Based on the Kruskal-Wallis Analysis of Variance by Ranks

	CalCOFI		ICHS		
	Nine concurrent cruises		8- & 22-m isobaths across 20 months		
Transect	*Engraulis* larvae ranking		*Engraulis* larvae ranking	*Engraulis* egg ranking	*Sardinops* larvae ranking
80	5	5	10	10	10
81.5			3	3	8
83	4	4	1	1	3
85			6	6	7
87	3	2	7	2	1
88			2	4	2
90	1	3	8	9	6
91			5	7	9
93	2	1	9	5	5
95			4	8	4
	$p<0.01$	$p<0.02$	$p<0.30$	$p<0.001$	$p<0.01$

The probability of equal transect ranks is indicated below each column.

cance of the transect differences. All station data from the complementary cruises were used to calculate mean transect abundance for each CalCOFI and ICHS cruise. Transects were ranked, and the ranks were summed across cruises for both CalCOFI and ICHS data. The results of the Kruskal-Wallis one-way analysis of variance by ranks (Siegel 1956) showed that transect ranks were significantly different (Table 7).

While a north (low)-to-south (high) gradient in abundance was suggested by the above rankings, a similar analysis of transect abundance within the ICHS region, which encompasses data from all seasons, showed different results. Table 6 summarizes ICHS transect data on the basis of stations over the 8-m and 22-m isobaths during Phase I and Phase II. We tested the rank sums of larval abundance for 10 transects across 20 months by the Kruskal-Wallis test as above. The 10 transects were not significantly different ($p<0.30$ of being equal), and no pattern or gradient was evident.

Northern Anchovy Eggs

Available data on *E. mordax* eggs are summarized in Tables 3 and 4. The highest mean density of eggs within the ICHS region was found in October 1978. However, over 99 percent of the eggs collected during the month were found along one transect (83), where stations over the 22-m and 36-m isobaths (4.5 km apart) yielded 997 and 17,904 eggs$\cdot m^{-1}$, respectively.

TABLE 6

Transect Data on Northern Anchovy Egg and Larval Abundance along 8-m and 22-m Isobaths within the ICHS Region

	Engraulis larvae						*Engraulis* eggs					
	Phase I & II			Phase II			Phase I & II			Phase II		
Transect	# Sta./ positive	$\bar{x}$ larvae $\cdot m^{-2}$	Std. dev.	# Sta./ positive	$\bar{x}$ larvae $\cdot m^{-2}$	Std. dev.	# Sta./ positive	$\bar{x}$ eggs $\cdot m^{-2}$	Std. dev.	# Sta./ positive	$\bar{x}$ eggs $\cdot m^{-2}$	Std. dev.
80	40/30	32.2	111.0	24/19	47.9	141.0	40/12	4.0	21.5	24/06	6.3	27.8
DR	—	—	—	24/17	52.0	141.3	—	—	—	24/13	37.1	167.8
81.5	40/31	29.4	66.6	24/18	36.2	82.6	40/27	15.0	43.3	24/18	21.9	54.8
RN	—	—	—	24/24	82.6	171.9	—	—	—	24/21	277.1	697.7
83	40/40	45.6	86.9	24/24	60.7	108.0	40/36	240.1	522.5	24/22	252.1	622.1
OB	—	—	—	24/23	43.8	97.7	—	—	—	24/24	137.6	199.7
85	40/38	20.5	38.6	24/23	21.6	45.7	40/31	52.0	235.7	24/22	83.7	302.6
MU	—	—	—	24/23	46.0	114.8	—	—	—	24/16	34.7	100.8
87	38/33	39.4	69.0	24/21	41.4	74.3	38/27	156.4	776.4	24/19	247.3	972.8
RB	—	—	—	24/21	31.8	54.8	—	—	—	24/11	30.1	71.5
PV*	—	—	—	24/21	17.2	27.9	—	—	—	24/15	12.9	20.8
88	40/39	27.6	48.5	24/23	30.6	57.8	40/30	56.6	163.9	24/20	89.4	206.5
BA	—	—	—	24/19	19.2	45.1	—	—	—	24/16	8.3	16.3
90*	40/35	24.3	58.1	24/20	29.7	73.1	40/22	5.6	16.3	24/12	3.2	6.7
SO	—	—	—	24/20	26.5	66.7	—	—	—	24/16	22.3	85.3
91	40/35	23.6	50.9	24/22	28.2	61.3	40/23	44.1	134.2	24/14	21.3	46.6
CD	—	—	—	24/18	30.1	70.2	—	—	—	24/12	3.8	8.8
93	39/30	39.6	72.6	24/18	36.3	66.3	39/17	15.3	74.9	24/10	2.9	7.1
MB	—	—	—	24/18	21.3	45.8	—	—	—	24/11	4.3	11.5
95	40/35	17.7	32.7	24/20	16.7	31.9	40/28	30.1	84.8	24/16	17.8	52.3

*Data from 15-m isobath substituted for unavailable 8-m data.

The graph of anchovy egg abundance versus station depth (Figure 6) shows points that both include and exclude the catch of eggs at transect 83, 36-m isobath during October 1978. Also included in the graph are average abundance of eggs per unit volume of water. The mean density of eggs throughout the water column decreased between the 22-m and 36-m isobaths, probably because of their relatively shallow vertical distribution, as noted for the larvae.

Longshore variability of eggs, based on mean transect abundance along the 8-m and 22-m isobaths (Table 6), approached two orders of magnitude. The highest spawning activity occurred in the region off transect 83, as well as transects 87 and 88. The rank differences between transects were highly significant ($p<0.001$) based on the Kruskal-Wallis test as described above (Table 7). The longshore rank of anchovy larvae was related to the longshore rank of anchovy eggs ($p<0.20$) based on the Kendall coefficient of concordance ($w=0.80$) (Siegel 1956). Also, monthly mean egg abundance corresponded reasonably well with mean larval abundance (Figure 7).

Comparisons of egg abundance between ICHS and CalCOFI regions require additional data. Since the 1980 CalCOFI cruises were not sorted for eggs, data from only five concurrent cruises were available. The CalCOFI 0.505-mm mesh net may underestimate egg abundance by a factor of three or more as a result of extrusion, compared to the 0.333-mm mesh net used by ICHS (Smith, P. 1975. Time series of the abundance of anchovy eggs in the California Current region. Admin. Rep. Unpub.).

Pacific Sardine Larvae

Sardine larvae occurred infrequently during most months. Overall, 18 percent of the 861 ICHS samples captured sardine, but estimates of abundance during some months may be reliable only on a presence/absence basis. However, the increase in the number of stations within the ICHS region where sardine larvae occurred between 1978-79 and 1979-80 is noteworthy. Tables 3 and 4 suggest that sardine may have moved from offshore in 1978 to onshore during 1979, but this observation is based on only eight occurrences within the CalCOFI region.

The abundance of sardine larvae as a function of bottom depth within the ICHS region as shown in Figure 8 was based on 453 samples with 73 occurrences, i.e., the same sample data set used to summarize anchovy egg and larval abundance in Figures 3 and 6. These data indicate that the mean density of larvae was highest at the 15-m isobath.

Between June 1978 and July 1979, sardine larvae were found most often along transects 87, 88, 93, and 95; no larvae were found north of transect 85. By September and October 1979, sardine larvae were captured at ICHS stations throughout the bight. Transects from Santa Monica Bay to Seal Beach yielded frequent catches during 1980 (Table 8). A noteworthy peak in estimated abundance in May 1980 resulted primarily from a large number of larvae at the 22-m

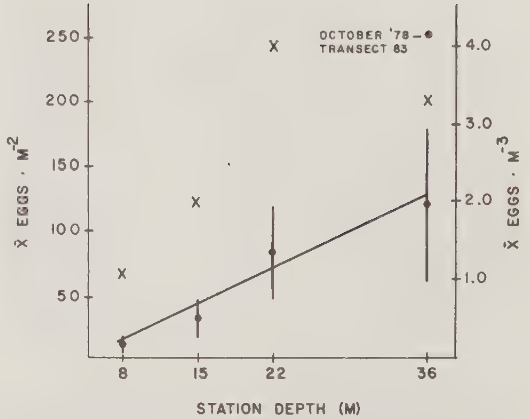

Figure 6. Average abundance per m^2 and 95 percent confidence intervals of northern anchovy eggs by station depth within the ICHS region ($Y=-22.03+4.12X$). The points and X's represent data from stations as described in Figure 3 with one exception: the datum from October 1978 transect 83, 36-m isobath was not included, as indicated. Inclusion of the one large sample gives a mean of 7.59-m^{-3} for the 36-m isobath.

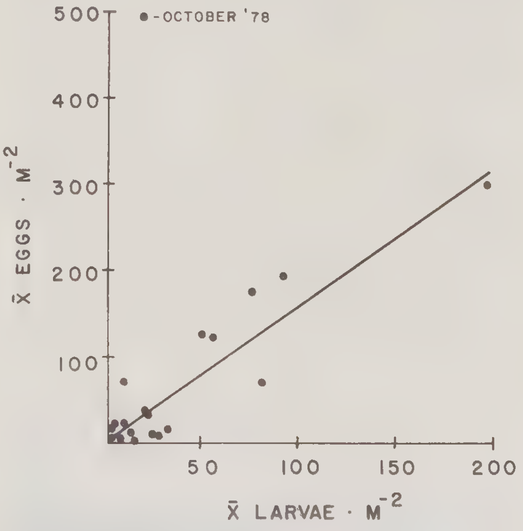

Figure 7. Average abundance of northern anchovy eggs versus larvae for each ICHS cruise ($Y=3.51+1.58X$; $r^2=0.84$). The October 1978 data were omitted.

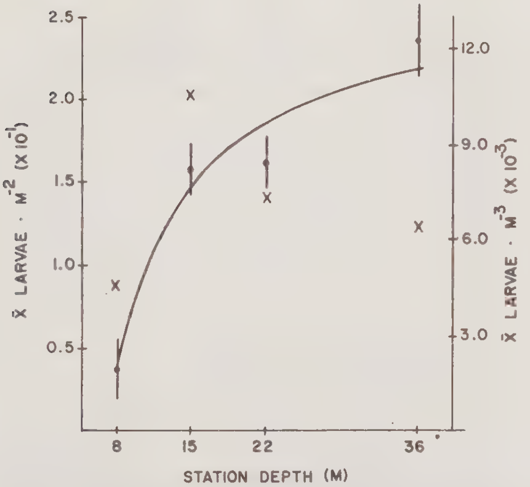

Figure 8. Average abundance per m² and 95 percent confidence intervals of Pacific sardine larvae by station depth within the ICHS region ($Y=0.27-1.88/X$; $r^2=0.95$). The points and X's represent data from stations as described in Figure 3.

TABLE 8
Transect Data on Pacific Sardine Larvae Abundance along 8-m and 22-m Isobaths within the ICHS Region

	Phase I & II			Phase II		
Transect	# Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.	#Sta./ positive	$\bar{x}$ larvae •m^{-2}	Std. dev.
80	40/01	0.005	0.034	24/01	0.009	0.04
DR	—	—	—	24/01	0.01	0.05
81.5	40/02	0.01	0.05	24/02	0.02	0.07
RN	—	—	—	24/05	0.07	0.16
83	40/06	0.29	0.98	24/06	0.48	1.24
OB	—	—	—	24/04	0.06	0.17
85	40/03	0.14	0.73	24/02	0.22	0.94
MU	—	—	—	24/07	0.35	0.87
87	38/14	0.44	1.10	24/11	0.65	1.34
RB	—	—	—	24/12	0.55	1.22
PV*	—	—	—	24/12	0.72	1.55
88	40/10	0.85	3.93	24/09	1.40	5.04
BA	—	—	—	24/04	0.09	0.29
90*	40/04	0.04	0.15	24/03	0.05	0.16
SO	—	—	—	24/03	0.05	0.14
91	40/01	0.05	0.34	24/01	0.09	0.44
CD	—	—	—	24/05	0.08	0.18
93	39/05	2.17	12.41	24/03	3.43	15.80
MB	—	—	—	24/06	0.26	0.88
95	40/06	0.16	0.44	24/04	0.15	0.41

*Data from 15-m isobaths substituted for unavailable 8-m data.

station off Del Mar. The Kruskal-Wallis test showed that transect differences were significant ($p<0.01$).

The overall temporal abundance of sardine larvae within the ICHS region is of interest, especially as it compares with the abundance of anchovy eggs and larvae (Figure 9). If one considers the monthly time series during 1979-80, when the frequency of sardine occurrence was relatively high (and if one ignores the one large May 1980 sample), sardine larvae were most abundant during late summer and fall; anchovy were least abundant during this same period. Ahlstrom (1967) showed that (during the 1950s) sardine spawning during the second half of the year was confined to a southern population and to waters off central Baja California. One might speculate that the relatively large occurrence of sardine larvae in the late summer and fall indicated that some southern fish had moved north and contributed to the peak abundance of sardine larvae off southern California. If a similar seasonal spawning cycle persists in subsequent years, CalCOFI surveys conducted during the first half of the year to monitor anchovy spawning may miss peak abundance of sardine larvae off southern California.

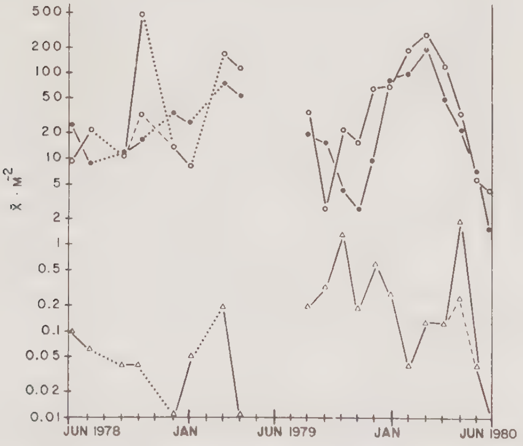

Figure 9. Temporal distribution of northern anchovy eggs (circles), larvae (dots), and Pacific sardine larvae (triangles) within the ICHS region. Dotted lines span months without data. Dashed lines indicate exclusion of unusually large samples from October 1978 transect 83, 36-m isobath (anchovy eggs) and May 1980 transect 93, 22-m isobath (sardine larvae).

DISCUSSION

The spawning habitat of the central subpopulation of northern anchovy extends over 500,000 km² of ocean—roughly between central Baja California and central California—but changing environmental factors apparently restrict the majority of spawning activity to much smaller regions during any one season. Major onshore-offshore and north-south shifts in larval abundance are evident during some years (Hewitt 1981; Smith and Eppley 1981). Broad temporal and spatial variability is a recurring feature of northern anchovy spawning; 20 months of ICHS data spread over 26 months should be interpreted in this context.

Since 1966, the area between Pt. Conception and

San Diego (primarily region 7) has accounted for an average of 64 percent of all larvae from the central subpopulation (Hewitt 1981). Based on the above percentage and the ICHS census estimates, about 2 percent of all anchovy larvae spawned by the central subpopulation were found in the ICHS region. Because densities of anchovy larvae were comparable in concurrent ICHS and CalCOFI cruises, inclusion of ICHS data with existing CalCOFI region 7 data would do little to alter overall abundance estimates used for biomass calculations (Pacific Fishery Management Council 1978). We conclude that the nearshore region off southern California was not a preferred habitat for the adult spawning biomass of northern anchovy during 1978-80. Smith and Duke (1975) reached a similar conclusion on the basis of CalCOFI cruises that sampled nearshore stations during 1964.

Anchovy spawning activity in the ICHS region indicates activity in larger CalCOFI regions. For example, changes in total number of larvae in region 7 were reflected by proportional changes in the ICHS region (Figure 2). Moreover, average density of larvae in ICHS samples during 1979-80 (Phase II) increased 31 percent compared to 1978-79 (Phase I); CalCOFI estimates of larval abundance for the entire central stock increased 36 percent during the same period (Stauffer and Picquelle 1981).

The apparent increase of sardine larvae in nearshore waters is of interest, but data are too infrequent to estimate what proportion of the larvae were spawned in respective ICHS and CalCOFI regions.

A direct relationship is presumed to exist between the abundance of planktonic eggs and larvae of northern anchovy and Pacific sardine and the size of their respective spawning stocks (Smith 1972; Smith and Eppley 1981; Parker 1980). However, numbers of eggs and larvae that survive to recruitment may vary independently of stock size, apparently influenced by environmental factors that are not understood or measured (Lasker and Smith 1977; Lasker 1978; Smith 1978; Bakun and Parrish 1980). The number of larvae that survive to recruitment within the shallow coastal region, i.e., the region's importance as a nursery ground, is not yet clear. Recruitment from any particular region may not be a direct function of the abundance of eggs or young larvae within the area because the environmental factors that favor spawning of adult anchovy (temperatures of 13-18°C and an abundance of available calories, such as large zooplankters) may not coincide with the environmental requirements for larval survival, which include patches of unarmored dinoflagellates or copepod nauplii in a stable ocean, and the absence of predators such as certain large zooplankters and adult anchovy (Hewitt 1982). Currents might transport eggs or young larvae away from spawning grounds to areas favorable or unfavorable for survival (Hunter 1977; Lasker and Smith 1977; Lasker 1978; Hewitt and Methot 1982).

The abundance of eggs and larvae within the ICHS region was consistently greater in certain areas. Transects within the Santa Barbara Channel from Rincon through Ormond Beach were important regions of anchovy spawning, as were transects off Playa Del Rey and Seal Beach. Sardine larvae occurred most frequently at transects throughout Santa Monica Bay and downcoast off Palos Verdes and Seal Beach. Cojo Bay yielded the least anchovy and sardine.

A discussion of environmental features common to the nearshore transects where large numbers of eggs and larvae were found is beyond the scope of this paper; indeed, such a discussion would be premature until we describe how the length-frequencies of the larvae vary between transects; i.e., are large larvae found consistently along certain transects?

Preliminary length-frequency data from ICHS stations show relatively large numbers of 20-30-mm anchovy larvae; larvae in similar size classes are virtually nonexistent in CalCOFI samples (Hewitt, pers. comm.).

We emphasize that the inherent imprecision of sampling fish eggs and larvae over wide areas leads to biases that must be identified and, if possible, quantified before one can understand the relative nursery function of the ICHS nearshore region. For northern anchovy and sardine larvae, these biases may include escapement and extrusion through the meshes of the net and avoidance of the net mouth. These and other factors, such as temperature, that result in sampler catch bias have been discussed by Zweifel and Smith (1981), who offer larval size-specific adjustment factors for correcting raw survey data. Hewitt and Methot (1982) have recently adopted these techniques for 1978 and 1979 CalCOFI data.

If the number of surviving larvae is proportionally greater, relative to numbers of eggs spawned, in the nearshore region versus offshore areas, or between nearshore transects, the techniques of Zweifel and Smith (1981) should be sensitive to such differences. We plan to test these hypotheses in the near future.

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FOUR NEW SPECIES OF SQUID (OEGOPSIDA: *ENOPLOTEUTHIS*) FROM THE CENTRAL PACIFIC AND A DESCRIPTION OF ADULT *ENOPLOTEUTHIS RETICULATA*

LOURDES ALVINA BURGESS[1]

ABSTRACT

Four new species of *Enoploteuthis* (*E. obliqua, E. octolineata, E. jonesi,* and *E. higginsi*) are described, illustrated, and compared. Adults of *E. reticulata* Rancurel 1970 are described for the first time. A key for all the species is provided.

Cephalopods are important fisheries resources in the Pacific Ocean. Thus, clarification of cephalopod systematics, particularly from areas where they are not thoroughly known such as the central Pacific, is important. Because enoploteuthid squids are deepwater animals that are not easily accessible or profitable to fish, they are not at present generally exploited commercially. In Toyama Bay, Sea of Japan, however, the enoploteuthid squid *Watasenia scintillans* (Berry 1911) is fished regularly in the spring and early summer when swarms of this species migrate to the surface to spawn (Sasaki 1914).

Cephalopods also play important roles in marine food webs. They are the principal food of many marine mammals, fishes, and some birds. Reintjes and King (1953) found that 26% of the aggregate total volume of the stomach contents of yellowfin tuna, *Thunnus albacares*, captured in the central Pacific consisted of cephalopods. King and Ikehara (1956) showed that as much as 33% of the food of the bigeye tuna, *T. obesus*, were squids, including *Enoploteuthis* sp.

Berry (1914) reported on the cephalopods collected on board the U.S. Fish Commission steamer *Albatross* from the Hawaiian area; the collection included enoploteuthid squids but none of them of the genus *Enoploteuthis*. Species of *Enoploteuthis* from Hawaiian waters and the central Pacific are described here for the first time and compared with all the known species of *Enoploteuthis* in the world.

Four new species of pelagic squids belonging to the genus *Enoploteuthis*, together with some adults of *E. reticulata*, were identified during the examination of the large collection of cephalopods at the Honolulu Laboratory, Southwest Fisheries Center of the National Marine Fisheries Service (NMFS), Honolulu, Hawaii (formerly Bureau of Commercial Fisheries Biological Laboratory, Honolulu).

The squids were taken from various areas of the central Pacific on several research vessels operated by the Honolulu Laboratory from 1953 to 1970. The fishing gear was either a modified Cobb trawl, a 10-ft Isaacs-Kidd trawl, or a Nanaimo trawl. The depth of fishing generally was between 50 and 100 m; most of the fishing was done at night.

Details on the capture of the cephalopods reported on here, including all holotypes and paratypes, are available from the original cruise reports and logs on file at the Honolulu Laboratory.

Type specimens are deposited in the cephalopod collections of the Division of Mollusks, U.S. National Museum of Natural History (USNM), Smithsonian Institution.

The terminology of the anatomical parts, measurements, and indices conform to those generally used for squids and in particular to those listed and defined by Roper (1966): ML = mantle length, CH = club hooks, CS = club suckers, MWI = mantle width index, HWI = head width index, FLI = fin length index, FWI = fin width index, ALI = arm length index, and TLI = tentacle length index. As in Roper (1966) the arm length is measured from the first basal hook (or sucker) to the tip of the arm.

The ranges and means of indices given in the descriptions were computed from measurements of the male and female specimens listed in Tables 1 to 5. This is not applicable to indices in-

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii; present address: T. F. H. Publications, Inc., 211 West Sylvania Avenue, Neptune, NJ 07753.

Manuscript accepted April 1982.

cluded in the remarks on immature individuals; not all their measurements are presented in the tables.

The following abbreviations which appear in the list of material refer to the research vessels: HMS = *Hugh M. Smith*, CHG = *Charles H. Gilbert*, and TC = *Townsend Cromwell*. A + sign after numbers in the text and tables indicates a missing mantle or arm tip, or lost suckers.

FAMILY ENOPLOTEUTHIDAE PFEFFER 1900

Genus *Enoploteuthis* Orbigny 1848

Diagnosis: Enoploteuthids with numerous light organs on mantle, head, and arms; single row of small light organs on ventral surface of eyeball; two rows of hooks on tentacular club; buccal connectives DDVD[2]; fins lateral; and mantle projecting posteriorly as free "tail."

Type species: *Loligo leptura* Leach 1817; Hoyle 1910:409, by elimination.

Enoploteuthis obliqua n. sp.

(Figs. 1, 2A; Table 1)

Enoploteuthis sp. (No. 2), Okutani 1974: figures 12c, d, f.

Holotype: Male, ML 55 mm, TC-48, Stn. 11, 11°47′N, 144°47′W, 31 March-1 April 1970, 50 m, USNM 729722.

Paratypes: 1 female, ML 50 mm, TC-46, Stn. 9, 11°49′N, 144°51′W, 14 October 1969, 50 m, USNM 577605. 1 male, ML 41 mm, TC-46, Stn. 9, 11°49′N, 144°51′W, 14 October 1969, 50 m, USNM 729713. 1 male, ML 58 mm, TC-48, Stn. 19, 11°34′N, 144°54′W, 3-4 April 1970, 50 m, USNM 729688.

Other material: 5 specimens, ML 12-17 mm, TC-43, Stn. 10, 12°03′N, 144°55′W, 8 May 1969, 50 m. 16 specimens, ML 5-18 mm, TC-43, Stn. 14, 11°56′N, 144°56′W, 10 May 1969, 50 m. 5 specimens, ML 12-17 mm, TC-43, Stn. 22, 07°41′N, 145°01′W, 13 May 1969, 50 m. 1 female (from *Alepisaurus* stomach contents), ML 50 mm, TC-44, equatorial central Pacific, July-August 1969, 10-100 m, USNM 729716. 2 specimens, ML 5 and 10 mm, TC-44, Stn. 16, 11°51′N, 144°41′W, 11 July 1969, surface. 1 specimen (from *Alepisaurus* stomach contents), ML 27 mm, TC-44, Stn. 17, 11°N, 144°W, 10 July 1969. 2 specimens, ML 12 and 17 mm, TC-44, Stn. 18, 11°53.2′N, 144°49.3′W, 11 July 1969, 100 m. 1 male, ML 37+ mm, 4 specimens, ML 12-20 mm, TC-44, Stn. 24, 07°32.9′N, 145°58′W, 13 July 1969, 50 m. 1 specimen, ML 13 mm, TC-44, Stn. 32, 07°31.5′N, 144°50.2′W, 17 July 1969, 50 m. 1 specimen, ML 12 mm, TC-44, Stn. 54, 00°01.8′N, 145°08.8′W, 28 July 1969, 50 m. 4 specimens, ML 6-11 mm, TC-47, Stn. 16, 12°02′N, 144°54′W, 23 January 1970, 50 m. 3 specimens, ML 7-10 mm, TC-48, Stn. 16, 11°45′N, 144°46′W, 2-3 April 1970, 20 m. 1 female, ML 40+ mm, TC-48, Stn. 19, 11°34′N, 144°54′W, 3-4 April 1970, 50 m.

Description: The mantle is muscular except for the thin-walled posterior end (tail) consisting of a gelatinous alveolar material. The mantle is widest (MWI 29.1-*32.4*-34.1) at the anterior edge and tapers into a blunt end. The anterior ventral margin is slightly excavated forming low, pointed lateral angles on each side. The dorsal margin is extended anteriorly into a median rounded lobe.

The fins are wider (FWI 62.1-*69.5*-73.2) than their lengths (FLI 52.0-*59.0*-64.0). They are attached anteriorly at about the midpoint of the mantle length. The anterior margin of each fin forms a rounded lobe. The lateral angles (72°) of the fins are rounded. The posterior margins are straight and are fused to the mantle separately, except for a point (difficult to see) near the tip of the mantle where they join.

The funnel is large, triangular, and has a broad base. The funnel-mantle locking cartilage is straight, the ends are rounded but the anterior end is slightly narrower; the median groove is shallow. The funnel organ of the holotype is large (9 mm long). The dorsal pad has an inverted V-shape with a slender papilla anteriorly and with prominent ridges on the limbs; each limb is about 2.5 mm wide. The ventral pads are oval and elongated (7 mm long, 3 mm wide).

The head is nearly square in cross section and narrower than the mantle (HWI 21.8-*26.0*-29.3). The funnel groove has a distinct edge on each side. The edges continue posteriorly to form the first pair of nuchal folds which bears the small olfactory papillae. The second and third nuchal folds are crescentlike membranes on each side

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[2] D = dorsal; V = ventral.

TABLE 1.—Measurements (in millimeters) and counts of *Enoploteuthis obliqua*. TC = RV *Townsend Cromwell*; + = a [illegible]

Cruise	[illegible]	[illegible]	[illegible]	TC-44	TC-46	TC-44	TC-44	TC-44
Station	19	11	9		9	24	24	18
		[illegible]						
Sex	Male	Male	Female	Female¹	Male	Male	?	?
Mantle length	[illegible]	[illegible]	[illegible]	50	41	37+	20	17
Mantle width	19	18	17	16	14	13	9	9
Head width	17	12	14	12	11	8	5.5	7
Fin length	34	32	[illegible]	32	21	17	7	8
Fin width	35	33	38	35	30	22	10	12
Arm length								
Right I	26	25+	25	26	[illegible]	17+	9	10
Right II	[illegible]	24	28	27	21	17+	12	11
Right III	28+	28	24	30	20	21+	11	9+
Right IV	31	27+	25	31	20	20+	10	9+
Left IV	32	27	25	31	22	22	10	—
Arm hooks/suckers								
Right I	18/24	25/24	23/28	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	22/20	20/18	20/—	17/—	18/13
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Right IV	28/16	30/27	32/[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Left IV	28/16	31/18	31/[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]								
Tentacle length	—	47/52	32/—	[illegible]	29/30	[illegible]	[illegible]	[illegible]
Club length	—	[illegible]	8.5/—	13/13	7/—	7/—	3.5/—	3.5/—
Club hooks								
[illegible]								
[illegible]	—	4/4-4/3	4/5/—	4/5-4/5	3/5-4/4	—	—	1/—
Club suckers [illegible]								
Distal suckers	—	—/13	17/—	14/14	11/—	11/—	—	—
Carpal suckers	—	5/3	5/—	5/5	5/5	4/4	3/4	5/—

¹ [illegible]

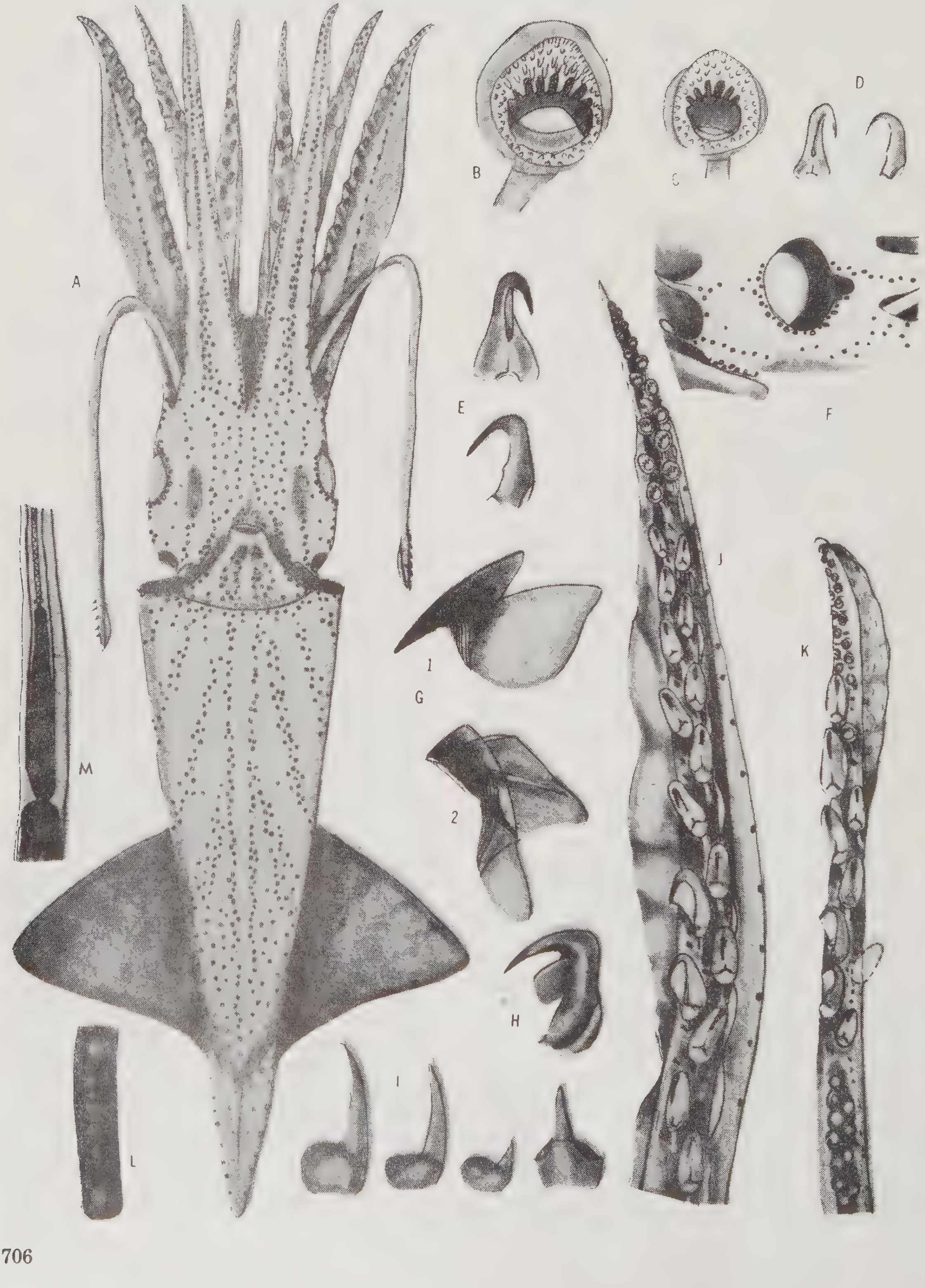
of the neck that are connected to each other posteriorly by a narrow membranous ridge. The third dorsal fold extends dorsally as a membranous ridge, but the ridge does not reach the midline of the head. Dorsal and ventral ocular "windows" are present and the latter easily allows a count of the nine eye photophores on the ventral side of the eyeball. The eye opening is a large, wide, transverse oval with a deep sinus (Fig. 1 F).

The buccal membrane completely hides the buccal mass and surrounding lips. Eight slender supports are joined by slender connectives to the arms in the order DDVD (i.e., all are attached to the dorsal side of the arms except the third pair which are attached to the ventral side of arm III). The inner surface of the buccal membrane is rugose, but without papillae; the lappets are delicate and pointed. The membrane is purple and does not appear much darker than most parts of the body. The chromatophores are small and are scattered evenly on both the supports and the membrane.

The arms are subequal, slender, and much shorter than the mantle length (ALI: I, 48.8-*50.2*-52.0; II, 43.6-*50.2*-54.0; III, 47.3-*51.0*-60.0; IV, 48.8-*53.2*-62.0). They taper gradually to slender tips. The swimming keels are low and poorly developed on the dorsal arms, and they are mainly confined to the distal third of these arms. The swimming keel of arm III is wider than the arm at its greatest width. The lateral membrane or tentacular sheath along arm IV is narrow; it is about half of the arm width proximally and it extends to the tip of the arm. Protective membranes are developed on the ventral side of all arms, but decrease in size in the following order: III, II, I, IV. The dorsal protective membranes on all the arms are low; on arm IV the trabeculae are not evident.

The right ventral arm of the male is hectocotylized. The protective membrane on the medial side of this arm (Fig. 1J) is expanded into an undulating membrane that extends from the eighth pair of hooks to the tip of the arm. The dorsal protective membrane is slightly developed. In the males small tubercles or conical papillae are present between the bases of the hooks and bases of all arms.

All the arms bear two rows of alternating strong hooks, each (Fig. 1E) completely enclosed in a membranous sheath. The distalmost hook is about half the length of the largest one. In both sexes, arm IV has the most hooks. The distal part of each arm is occupied by two rows of suckers with wide apertures and slender stalks. The inner sucker ring bears seven or eight prominent truncated teeth on the distal margin but the proximal margin is smooth (Fig. 1B). The outer ring has numerous pegs (Nixon and Dilly 1977).


A
B
C
D
E
F
G
1
2
H
I
J
K
L
M

The suckers decrease in diameter distally, become globular in shape, and have only three or four blunt teeth.

The tentacles are shorter than the mantle (TLI 62.1-*79.2*-96.4), very delicate and slender. The stalk is laterally compressed, about a third of the width of arm III. The club is not expanded (Fig. 1K). The carpus bears a series of four or five suckers and four, five, or seven pads, and the whole cluster is bordered by a very low ridge on each side. The manus includes a dorsal row of three or four sheathed hooks and a ventral row of four or five slightly larger similarly sheathed hooks (Fig. 1D). These two rows are very close to each other. Marginal suckers are absent. A medial sucker or two may be present in series with the hooks distally. The largest club hook is smaller than any of the arm hooks. The dactylus of the club is occupied by 11 to 17 suckers that are also arranged in two rows. They have long stalks and wide openings. The distal margin of the inner sucker ring bears six or seven slender blunt teeth and the outer sucker ring has numerous pegs (Fig. 1C). Protective membranes are absent. The aboral keel or dorsal membrane is narrow and, at most, about half the length of the club. The tip of the club is rounded and bears a short hoodlike membrane that conceals one or two of the suckers there.

There are two types of light organs on the integument: Large dark ones with pearly white centers and small white ones with very narrow outer pigmented rings. These photophores range in size from small (0.2 mm) to large (0.4 mm), and they are randomly interspersed with each other. The most distinctive feature of this species is the unique arrangement of the mantle photophores. Some of the rows are slanting or oblique (Fig. 1A), instead of the usual straight longitudinal rows described in most other *Enoploteuthis* species. Two median longitudinal rows (two to three photophores in width), separated by an intervening space lacking photophores, extend from the anterior edge of the mantle to the posterior tail. Photophores on the posterior part of the mantle are scattered, those on the anterolateral part are arranged in four oblique rows on each side of the median longitudinal rows. Except for the most posterior row, the oblique rows radiate from the anterior edge of the mantle. The edge of the mantle is lined by a transverse row in which the photophores are closer to each other ventrally than dorsally. A few isolated photophores are present on the dorsal surface of the mantle, none are present on the surface of the fins. The tail has a single row on each side; a few photophores occur on the ventral side, but none are present on the dorsal side.

FIGURE 1.—*Enoploteuthis obliqua* (A-F, K, and L from female paratype, ML (mantle length) 50 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Dorsal arm sucker; C, Tentacular sucker; D, Tentacular hook, oral and lateral aspects; E, Dorsal arm hook, oral and lateral aspects; F, Eye and surrounding area; G, Mandibles: upper (1), lower (2), male, ML 37 mm; H, Dorsal arm sucker, ex-*Alepisaurus* female, ML 50 mm; I, Radular teeth, male, ML 37 mm; J, Hectocotylus, male, ML 41 mm; K, Tentacular club; L, Eye light organs; M, Section of spermatophore, male holotype, ML 55 mm.

Six groups of photophores occur on the funnel: Two broad rows separated by a narrow midline space on the ventral side; a short row of six or seven light organs on each lateral margin (one or two photophores are present in the space between these rows posteriorly); and a group of photophores on each side of the bridles on the dorsal side of the funnel.

There are two patches of light organs, separated by a narrow space, in the apical region of the funnel groove. Six rows are recognizable on the ventral surface of the head, three rows on each side of a narrow midline space devoid of photophores. A row (two or three closely set photophores in width) along the lateral edge of the funnel groove extends anteriorly with increased numbers of photophores medial to each eye. It then bifurcates into two branches: one branch extends along the ventral aboral border of arm IV to a point opposite the last arm hook, the other branch continues distally along the base of the tentacular sheath to the tip of arm IV. The next lateral row of the head photophores extends from near the first nuchal fold anteriorly, although a short gap occurs opposite the lens of the eye at the ventral window, along the head and onto the edge of the tentacular sheath where it continues to near the tip of arm IV. The lateralmost row of the head extends from between the second nuchal fold to the posterior margin of the eye; it continues as a single row of closely set photophores along the edge of the eyelid ventrally to the ventral edge of the optic sinus (Fig. 1F). The dorsal edge of the eyelid is devoid of light organs. From the dorsal edge of the optic sinus the row proceeds along the base of the swimming keel of arm II almost to the tip of the arm. Some small white photophores occur near the eye region between the median and lateralmost rows.

Nine light organs occur in a single row on the ventral side of the eyeball (Fig. 1L). The terminal photophores are larger and are separated by a wide space from a row of seven much smaller ones that lie adjacent to one another.

The teeth of the radula are long and slender (Fig. 1I); the rachidian has distinct cusps on each side. The first lateral teeth are the shortest.

The mandibles of a young male (ML 40 mm) have distinct growth lines on the wings. The rostrum is heavily pigmented; the edges are sharp and the tip of the upper mandible is very pointed (Fig. $1G_1$). The gular plate of the lower mandible is strengthened by three stout ribs (Fig. $1G_2$).

The gladius has a strong rachis which is rounded anteriorly and thickened medially. The thin vanes are widest at about the midpoint of the total length. The rounded posterior cone is shallow and thin.

A single spermatophore was found in the spermatophoric sac of the holotype (ML 55 mm), and its measurements are given below:

Spermatophore segment	*Length (mm)*
Entire spermatophore	11.5
Spiral filament	4.5
Cement body	1.5
Sperm reservoir	5.5

The spiral filament is slightly sculptured at the aboral end by some irregular ridges. The cement body has a small collar at the oral end (Fig. 1M). A few spiral turns are visible behind the spermatophore cap.

Young individuals: Small specimens (ML 6.0-20.0 mm) are easily separated from other species of *Enoploteuthis* by the unique oblique rows of photophores on the mantle. Early development of the oblique rows are shown in Figure 2Aa and b in specimens ML 7 and 9 mm, respectively. Arm hooks are formed early; six to nine hooks are already present in the arms at ML 6.0 mm. But tentacular hooks appear much later; a ML 17 mm specimen has one tentacular hook and another (ML 20 mm) has none at all. Only two rows of suckers are present on the club.

Remarks: A female specimen tentatively assigned to this species (from the stomach contents of an *Alepisaurus*) exhibits certain features not observed in other specimens of the same or nearly the same size. The arm and tentacular hooks have flattened processes (Fig. 1H). Furthermore, this specimen shows a slight variation in the arrangement of photophores: some photophores occur on the median space of the mantle.

The closest species to *E. obliqua* is *E. leptura* (Leach 1817) from the Atlantic. Both *obliqua* and *leptura* have slender tentacles and clubs. There are few suckers (<20) arranged in two rows on their clubs. However, *obliqua* has fewer tentacular hooks (at most 9) while *leptura* has more (6-12). The carpal cluster is elongate and without prominent ridges in both species. Their spermatophores show similar characteristics: very little sculpture in the spiral filament and one small collar on the cement body.

The specific name *obliqua* reflects the arrangement of the mantle photophores. The oblique arrangement of light organs on the mantle was described earlier by Okutani (1974). His three immature specimens (ML 23.8-25.8 mm) from the EASTROPAC collection and a fourth specimen from the invertebrate collection of the Scripps Institution of Oceanography are all referable to *E. obliqua*. His material was collected in the eastern Pacific.

Distribution: Equatorial regions of the central and eastern Pacific.

Enoploteuthis octolineata n. sp.

(Figs. 3, 2C; Table 2)

Holotype: Female, ML 71 mm, HMS-47, Stn. 58, 02°56′N, 150°03′W, 4 November 1958, 212 m, USNM 577607.

Paratypes: 1 female, ML 75 mm, TC-43, Stn. 52, 00°01′N, 145°03′W, 28 May 1969, 50 m, USNM 729721. 1 female, ML 56 mm, TC-46, Stn. 37, 03°23′N, 145°04′W, 26 October 1969, 50 m, USNM 729720. 1 male, ML 46 mm, TC-48, Stn. 50, 03°29′N, 144°58′W, 17-18 April 1970, 50 m, USNM 729708.

Other material: 1 specimen, ML 10 mm, HMS-47, Stn. 51, 00°44′S, 149°46′W, 2 November 1958, 576 m. 1 specimen, ML 25 mm, HMS-47, Stn. 58, 02°56′N, 150°03′W, 4 November 1958, 212 m. 1 specimen, ML 15 mm, CHG-89, Stn. 5, 02°40′N, 157°31′W, 28 July 1966, 120-240 m. 1 specimen, ML 15 mm, TC-43, Stn. 12, 12°11′N,

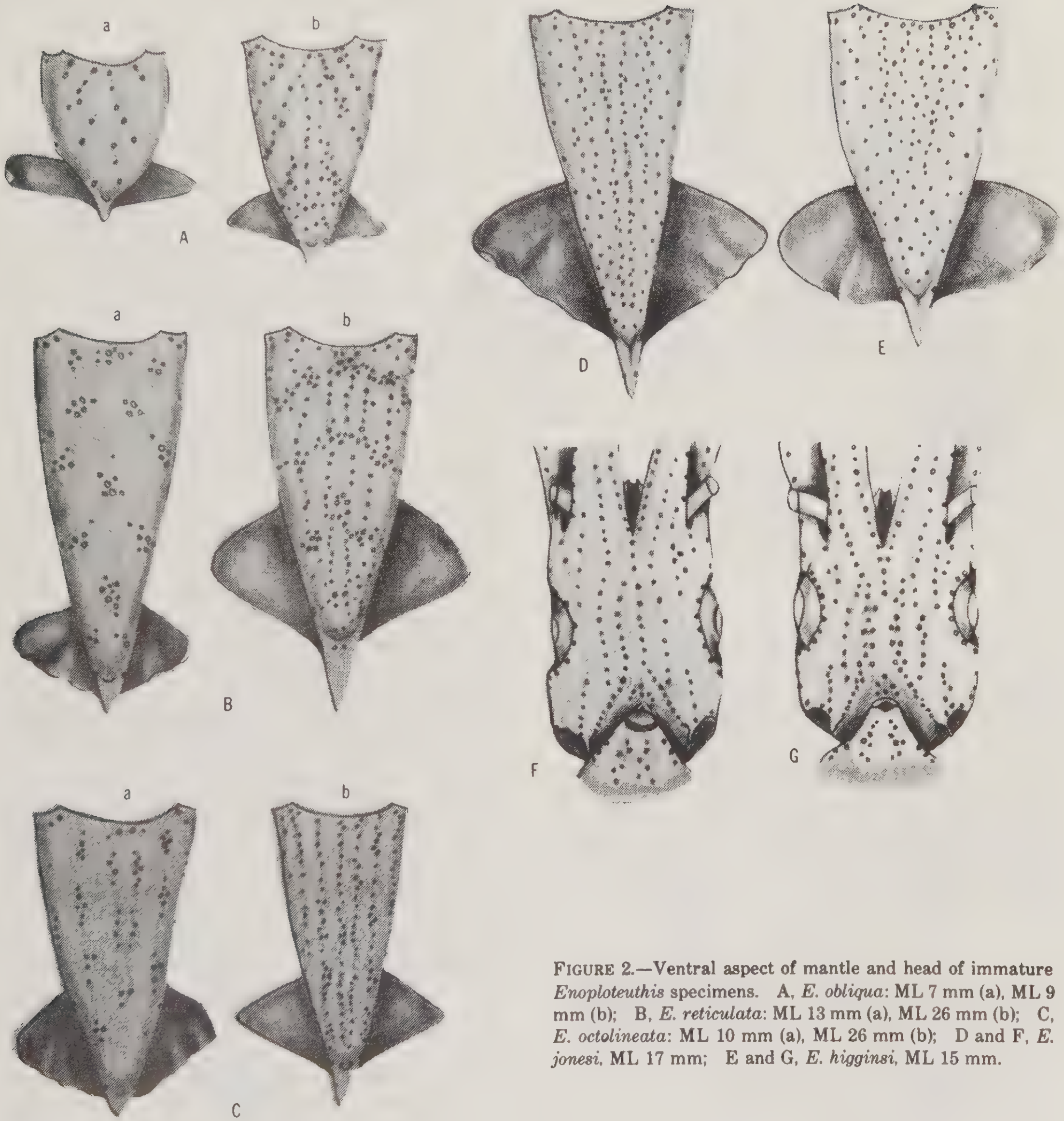


FIGURE 2.—Ventral aspect of mantle and head of immature *Enoploteuthis* specimens. A, *E. obliqua*: ML 7 mm (a), ML 9 mm (b); B, *E. reticulata*: ML 13 mm (a), ML 26 mm (b); C, *E. octolineata*: ML 10 mm (a), ML 26 mm (b); D and F, *E. jonesi*, ML 17 mm; E and G, *E. higginsi*, ML 15 mm.

145°11′W, 9 May 1969, 20 m. 1 specimen, ML 20 mm, TC-43, Stn. 26, 07°33′N, 144°50′W, 15 May 1969, 50 m. 3 specimens, ML 19-30 mm, TC-43, Stn. 38, 03°30′N, 145°06′W, 20 May 1969, 50 m. 2 specimens, ML 21 and 40 mm, TC-43, Stn. 42, 03°32′N, 144°59′W, 22 May 1969, 50 m. 1 specimen, ML 24 mm, TC-43, Stn. 48, 00°04′N, 145°07′W, 26 May 1969, 50 m. 2 specimens, ML 20 and 22 mm, TC-43, Stn. 52, 00°01′N, 145°03′W, 28 May 1969, 50 m. 1 specimen, ML 26 mm, TC-44, Stn. 26, 07°14.8′N, 144°58.8′W, 14 July 1969, 20 m. 1 specimen (from *Alepisaurus* stomach contents), ML 28 mm, TC-44, Stn. 44, 03°49.9′N, 145°18′W, 22 July 1969, 50 m. 1 specimen, ML 20 mm, TC-44, Stn. 56, 00°15.2′N, 144°43.9′W, 29 July 1969, 50 m. 1 specimen, ML 25 mm, TC-44, Stn. 68, 03°39′S, 144°54.5′W, 3 August 1969, 75 m. 1 specimen, ML 36 mm, TC-46, Stn. 41, 03°19′N, 145°03′W, 28 October 1969, 50 m. 2 specimens, ML 14 mm, TC-46,

TABLE 2.—Measurements (in millimeters) and counts of *Enoploteuthis octolineata*. HMS = RV *Hugh M. Smith*; TC = RV *Townsend Cromwell*; + = missing arm tips and lost suckers.

Cruise:	HMS-47	TC-43	TC-46	TC-48	TC-48	TC-44	HMS-47	TC-43
Station:	58	52	37	50	92	26	58	12
Sex:	(Holotype) Female	Female	Female	Male	?	?	?	?
Mantle length	71	75	56	46	33	26	25	15
Mantle width	26	27	21	18	13	11	13	6
Head width	24	21	16	14	10	10	12	5
Fin length	50	52	38	30	19	15	15	7
Fin width	54	56	42	32	23	20	20	8
Arm length								
Right I	43	49	28+	32	23	16	15	8
Right II	42	46	32	[1]32	24	16	18	8
Right III	42	50	31	38	25	18	17	7
Right IV	42	52	38	33	25	16	16	9
Left IV	45	54	35	31	25	18	16	—
Arm hooks/suckers								
Right I	21/36	23/26	20/23+	20/—	—	21/25	16/14	16/12
Right II	22/32	22/24	21/21	18/—	22/—	22/22	21/—	16/14
Right III	25/27	24/28	22/22	21/18	20/—	21/24	23/—	15/11
Right IV	29/25	34/38	32/25	29/23	28/10+	30/22	21/—	18/10
Left IV	30/30	32/34	31/26	29/20+	26/12	29/27	29/12	—
Tentacles right/left								
Tentacle length	75/80	70/70	53/—	43/44	39/37	15/16	25/—	13/—
Club length	19/18	—	14/15	12/13	10/9	5/5	5/—	4/—
Club hooks (Right (dorsal/ventral)-left (dorsal/ventral)	4/5-4/6	—-6/5	4/6-4/6	5/5-4/6	4/5-—	4/5-4/6	5/5-—	—
Club suckers right/left								
Distal suckers	16/17	—	14/14	14/16	10/—	—/19	—	—
Carpal suckers	3/5	6/4	6/5	5/6	4/—	6/4	3/—	—

[1]Length of left arm.

Stn. 45, 03°29′N, 144°54′W, 30 October 1969, 50 m. 1 female, ML 56 mm, TC-46, Stn. 47, 03°23′ N, 145°04′W, 31 October 1969, 115 m. 2 specimens, ML 16 and 20 mm, TC-47, Stn. 45, 03°28′ N, 144°59′W, 3-4 February 1970, 50 m. 1 specimen, ML 39 mm, TC-48, Stn. 35, 07°18′N, 144° 47′W, 11-12 April 1970, 50 m. 1 female, ML 49 mm, TC-48, Stn. 50, 03°29′N, 144°58′W, 17-18 April 1970, 50 m. 1 specimen, ML 33 mm, TC-48, Stn. 92, 00°08′N, 145°00′W, 28 April 1970, 50 m.

Description: The mantle (MWI 36.0-*37.3*-39.1) is cylindrical and tapers gradually toward the end of the blunt tail. Ventrally the anterior edge of the mantle is only slightly excavated and the lateral angles are pointed and low. The anterior dorsal lobe is rounded and also low.

The fin lengths are more than half of the mantle length (FLI 65.2-*68.0*-70.4) and the combined width of both fins is less than the mantle length (FWI 69.6-*73.9*-76.1). The anterior margins project into rounded lobes near their anterior attachments. The lateral angle (about 70°) is rounded and the posterior margin is slightly convex.

The funnel is large; its length equals its width. The funnel-mantle locking cartilage is simple; its anterior end is slightly narrower and more pointed than the rounder posterior end. The funnel valve is a wide semilunar flap; its anterior edge reaches the edge of the funnel opening.

The head (HWI 28.0-*30.2*-33.8) is narrower than the mantle, almost square in cross section, slightly rounded on the top, and is deeply excavated on its posteroventral surface to form a large funnel groove. The dorsal and ventral ocular "windows" are distinct. The eye opening has a deep sinus (Fig. 3G). Three nuchal folds lie on each side of the head; the closest fold to the funnel bears at its posterior end the tonguelike olfactory papilla. These nuchal folds are united to each other by a narrow posterior membrane, although this membrane does not reach the dorsal midline.

The buccal membrane is purple and the eight supports are joined by connectives to the arms in the order DDVD. The membrane is pigmented more heavily than the supports. The lappets are delicately pointed, and the inner surface of the buccal funnel is very rugose but lacks papillae.

The arms are subequal and shorter than the mantle (ALI: I, 60.6-*65.2*-69.7; II, 57.1-*61.8*-69.6; III, 55.4-*66.0*-82.6; IV, 59.2-*66.7*-72.0). They are nearly square at their bases and taper into fine points. Arms I and II have very low keels; arm I is keeled to about half its length and arm II to

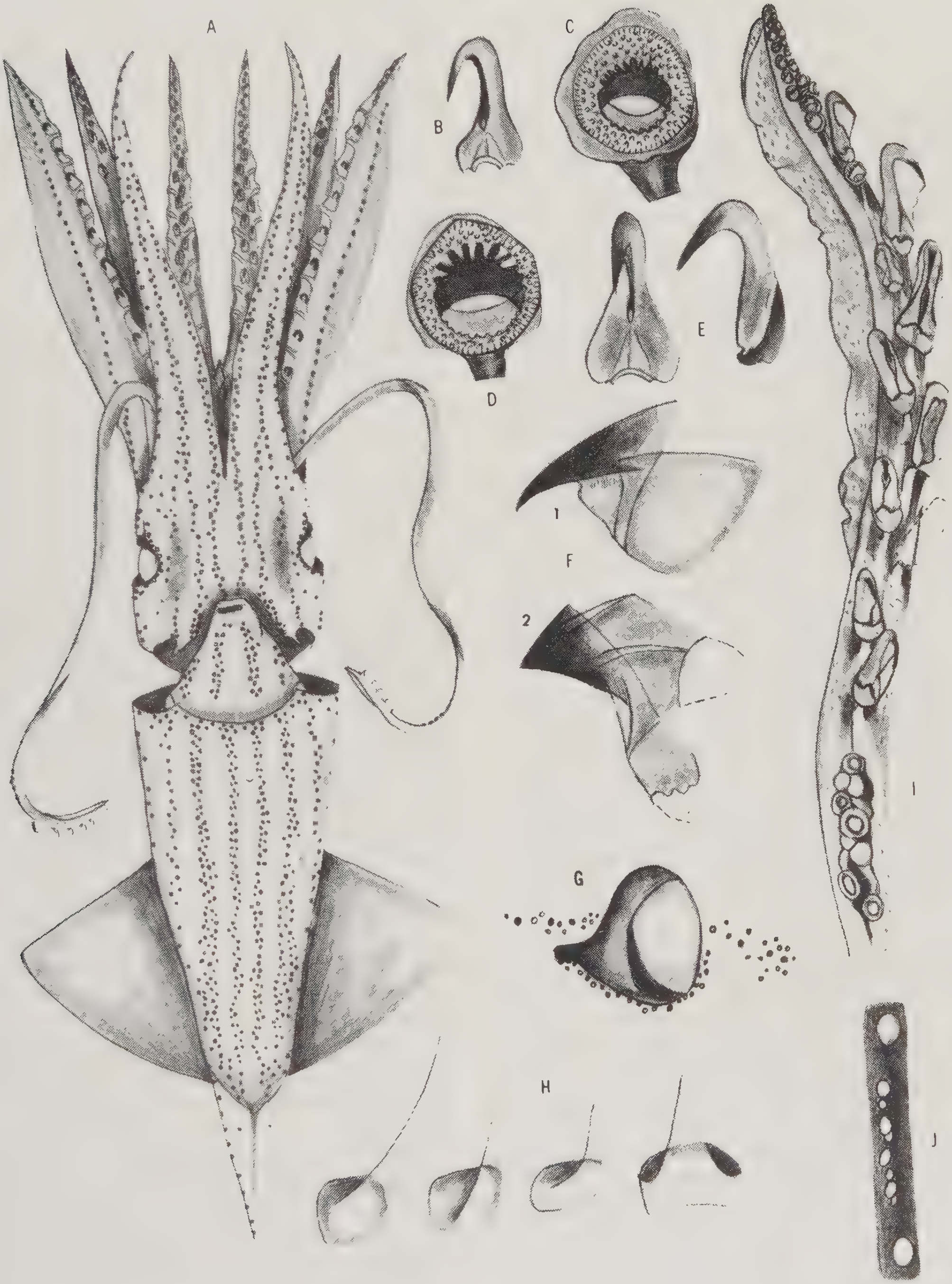


FIGURE 3.—*Enoploteuthis octolineata.* (A-E, G, I, and J from female paratype, ML (mantle length) 75 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Tentacular hook; C, Tentacular sucker; D, Dorsal arm sucker; E, Dorsal arm hook, oral and lateral aspects; F, Mandibles: upper (1), lower (2), male, ML 25 mm; G, Eye and surrounding area; H, Radular teeth, ML 25 mm; I, Tentacular club; J, Eye light organs.

about one-third. The swimming keel of arm III is about as wide as the arm. The tentacular sheath is narrow, about half the width of arm IV near the base. The dorsal and ventral protective membranes are developed on all the arms and extend to the arm tips. The ventral membranes are wider on arm III, although they do not reach the top of the hooks. The protective membranes of arm IV are very narrow, except those on the hectocotylus of the male.

The ventral protective membrane of right arm IV (hectocotylus) of the immature male paratype (ML 46 mm) is slightly enlarged into a narrow undulating membrane, about 1 mm wide, opposite the eighth and ninth pairs of hooks. The dorsal protective membrane is very narrow.

The arm hooks (Fig. 3E) are biserial and are completely covered by sheaths. Arm IV is slightly longer than the other arms, and has the greatest number of hooks. The suckers on the distal part of the arms can be separated into two types. The distalmost suckers are markedly reduced in size, are globular in shape with small apertures, and lack teeth. The proximal suckers have long stalks and wide openings. The inner rings of these suckers have eight to nine large pointed teeth distally, very irregular, smaller teeth proximally, and a wide shelf at the bottom half. The outer ring bears numerous pegs (Fig. 3D).

The tentacles are weakly developed, about as long as the mantle (TLI 93.3-*98.4*-112.7) and very narrow (only about one-third of the width of arm III). The cross section is almost triangular. The club is also narrow (Fig. 3I). The aboral keel extends from opposite the second hook to the tip of the club. Protective membranes are absent, but a short hoodlike membrane is present at the blunt tip. The carpal cluster is composed of a series of three to six smooth-ringed suckers and three to five rounded pads which are biserially arranged in an elongate patch. One of the paratypes (ML 75 mm) has two additional suckers on the stalk located a short distance from the right carpal cluster (such suckers not present in other specimens); corresponding pads, if any, were not seen on the opposite tentacle due to damage. The manus has a total of 9 to 11 sheathed hooks and an occasional sucker in the distal part. These alternating dorsal and ventral hooks are only slightly separated medially. Hooks on the dorsal row are smaller. The hooks (Fig. 3B) resemble the arm hooks in structure, except for the relatively narrower bases of club hooks and their relatively smaller size. The few (16 or 17) distal suckers on the dactylus are also biserial. They have long stalks and wide openings; the inner rings have about 10 sharp teeth distally, a series of smaller denticulations proximally, and an inner shelf at the proximal bottom part (Fig. 3C). The outer ring bears pegs.

There are two types of skin photophores: Very dark ones with whitish centers and white ones with very thin outer black rings (in preservation). The smallest is about half the size of the largest, but intermediate sizes occur. Both types appear randomly interspersed. On the ventral side of the mantle there are eight distinct rows separated by spaces wider than the rows themselves. A continuous midline space is present from the anterior of the mantle to the tail (Fig. 3A). Four parallel rows of varying widths lie on either side of this space. The first and second lateral rows extend from the excavated part of the mantle to the tail. The third row extends from opposite the lateral angle of the mantle to the tip of the mantle, occurring along the lateral margins of the tail as a single row of evenly spaced photophores. The photophores of these rows tend to disperse at the posterior end, particularly the second row, and the rows become slightly intermingled, but each row remains recognizable. The fourth or lateralmost row is composed of widely spaced light organs forming a single line that becomes somewhat irregular opposite the region of the fins. Small photophores are dispersed on the dorsal side of the mantle, but there are none on the fins or on most of the tail except for the lateral row mentioned above and a few very small ones ventrally. A transverse row that has fewer and more widely separated photophores dorsally runs along the edge of the mantle.

Four narrow rows of photophores separated by wide spaces are present on the ventral half of the funnel. There are two additional rows on the dorsal side, one on each side of the bridles.

There are eight separate rows of photophores on the ventral half of the head, four rows on each side of a wide median space. The first row lateral to the midline space originates anterior to the bridle within the apex of the funnel groove and continues directly to the ventral aboral side of arm IV and ends just beyond the distalmost arm hook. The second lateral row begins at the posterior end of the funnel groove and runs along the edge of the groove, over the ventral part of the head, and proceeds anteriorly along the base of the tentacular sheath to the tip of arm IV. The third row extends anteriorly from the base of the first nuchal fold but is interrupted by the window of the eye, and subsequently divides. One branch unites with the second row at a short distance from the base of the ventral arm. The other branch continues laterally along the edge of the tentacular sheath to the tip of arm IV. The fourth row begins opposite the second nuchal fold and proceeds to the posterior margin of the eye opening and runs along the edge of the eyelid ventrally to the optic sinus (Fig. 3G). The dorsal half of the eyelid has no light organs. From the upper edge of the optic sinus the fourth row continues along the base of the swimming keel of arm III to almost opposite the last arm hook. An additional short arc-shaped row of very small white photophores, set far apart, lies between the third and fourth rows on the posteroventral eye region. This short row is inconspicuous and can easily escape detection.

The light organs on the eyeball vary from 9 to 10. The large terminal photophores are separated by a space from a series of eight or seven adjacent round to oval smaller light organs (Fig. 3J) of varying dimensions.

The radula has seven long, slender, slightly curved teeth in each transverse row. The rachidian tooth has pointed cusps, one on each side. The lateralmost teeth are longest (Fig. 3H).

The mandibles are strong and heavily pigmented. The rostrum of the upper mandible is very pointed and the edges are sharp (Fig. $3F_1$). The lower mandible has three distinct ridges (Fig. $3F_2$). In a specimen ML 25 mm the wings of both halves are transparent.

The gladius is featherlike and the rachis is thickened into a rounded ridge dorsally. The vanes are fragile and narrow. The cone is thin and narrow, but rounded posteriorly. The thickened edge of the vanes described by Roper (1966, fig. 14) in *E. anapsis* is only slightly indicated here.

There are no spermatophores in the largest male paratype (ML 46 mm). The hectocotylus is not fully developed; the lappet is only 1 mm wide and there are no tubercles on the inner surface of the arms. Numerous sperm reservoirs are present in one of the females (ML 75 mm). These are about 6 mm long and are attached in two areas: on the inner wall of the mantle (opposite the midpart of each funnel retractor muscle) and in the concave inner wall of the retractor muscles themselves. The same female is gravid; the diameter of an egg taken from the ovary is slightly <1 mm.

Young individuals: Immature specimens (ML 10-30 mm) have six to eight rows of light organs on the mantle. These rows first appear as a series of elongate patches of large photophores separated by spaces which later develop smaller photophores (Figs. 2Ca, b). At ML 10 mm, all the arms have hooks. The club has two rows of suckers and no hooks. Five of the suckers are set apart proximally and presumably become carpal suckers. At ML 15 mm there are three hooks on the club; by ML 20 mm the club has eight hooks. The tentacles of these immature individuals are shorter than the mantle (TLI 50.0-*68.4*-86.7). The light organs of the eye do not develop simultaneously: some of the smaller individuals have only seven or eight (the two terminal photophores and five or six inner ones).

Remarks: The most distinctive feature of this species is the eight well-defined rows of photophores, separated by wide spaces, on the mantle. In some respects this species resembles *E. leptura* in the shape of the fins and the structure of the clubs and tentacles. However, the latter species has only seven rows of photophores on the mantle, one of which arises from either of the most median pair of rows and does not reach the mantle. This feature is also found in juveniles. The arrangement of the photophores on the head also differs. The third lateral row is unbranched in *E. leptura*.

Distribution: Central Pacific, equatorial waters. Based on sampling for the present collection, *E. octolineata* does not seem to occur in the Hawaiian area.

***Enoploteuthis jonesi* n. sp.**

(Figs. 4, 2D, F; Table 3)

Holotype: Male, ML 47 mm, TC-7, Stn. 12, off Milolii, Hawaii, 16 August 1964, 9-13 m, USNM 729717.

Paratypes: 1 male, ML 35 mm, CHG-89, Stn. 24, 14°55.1′S, 164°02′W, 10 February 1966, 90-130 m, USNM 729699. 1 female, ML 82 mm, TC-7, Stn. 12, off Milolii, Hawaii, 16 August 1964, 9-13 m, USNM 577608. 1 female, ML 40 mm, TC-32, Stn. 28, 20°58.6′N, 158°33.7′W, 25 July 1967, 92-122 m, USNM 729707.

Other material: 1 male, ML 27 mm, CHG-89, Stn. 14, 06°06.9′S, 157°44.2′W, 3 February 1966, 70-80 m. 1 specimen, ML 22 mm, CHG-89, Stn. 29, 04°05′S, 167°51′W, 14 February 1966, 120-135 m. 1 specimen, ML 17 mm, CHG-89, Stn. 31, 01°01′S, 168°06′W, 15 February 1966, 90-150 m. 1 specimen, ML 11 mm, TC-32, Stn. 37, 20°59.1′N, 158°12.7′W, 15 August 1967, 55-123 m. 1 female, ML 30 mm, TC-32, Stn. 39, 20°59.6′N, 158°29.3′W, 15 August 1967, 63-101 m. 1 female, ML 35 mm, TC-32, Stn. 46, 20°57.6′N, 158°28.7′W, 18 August 1967, 77-118 m.

Description: The mantle is long, cylindrical, and narrow (MWI 24.4-*34.3*-40.7). The width at the edge is only slightly greater than that at the middle and the sides taper into a blunt tail. The mantle is muscular except for the tail which is thin-walled and translucent, yet very firm. The ventral anterior excavation of the mantle is shallow and the lateral angles and middorsal projection are low and blunt.

Each fin is triangular and their combined width is about three-fifths to four-fifths of the mantle length (FWI 65.9-*74.0*-80.0). The fins are shorter than their combined width (FLI 62.9-*67.5*-70.0). The anterior margin is rounded and the posterior margin is slightly concave. The lateral angles are sharp, about 75°.

The funnel is triangular with a broad base. The funnel-mantle locking cartilage is simple and typical of the genus. The groove is shallow and it spreads out toward the more rounded posterior end of the cartilage. The funnel organ is large; the dorsal pad has a papilla and well-developed ridges; the ventral pads are oval with pointed anterior ends. The semilunar funnel valve is wide and its anteriormost edge does not reach the edge of the funnel opening.

The head is nearly square in cross section, as long as it is wide, and nearly as broad as the mantle (HWI 25.6-*30.9*-37.5). Both dorsal and ventral ocular "windows" are distinct. The eye opening is a wide oval (triangular when constricted) and has a moderately deep sinus. The three crescentic nuchal folds are prominent. The olfactory papilla is tonguelike and arises from the nuchal fold nearest to the funnel. The funnel groove is moderately deep and the sides of this excavation are steep.

The buccal funnel has eight stout supports connected to the arms in the order DDVD. The lappets are pointed; the inner wall of the buccal membrane is very rugose and carries papillae. Both membrane and supports are covered with small fine chromatophores, but the membrane appears darker.

The arms are of moderate length (ALI: I, 40.0-*45.4*-50.0; II, 43.9-*48.8*-51.9; III, 47.6-*51.3*-59.2;

TABLE 3.—Measurements (in millimeters) and counts of *Enoploteuthis jonesi*. TC = RV *Townsend Cromwell*; CHG = RV *Charles H. Gilbert*; + = lost suckers.

Cruise:	TC-7	TC-7	TC-32	CHG-89	TC-32	CHG-89	CHG-89	CHG-89
Station:	12	12	28	24	39	14	29	31
Sex:	Female	(Holotype) Male	Female	Male	Female	Male	?	?
Mantle length	82	47	40	35	30	27	22	17
Mantle width	20	14	15	13	11	11	10	9
Head width	21	13	15	11	9	9	8	6.5
Fin length	56	32	28	23	21	17	14	10.5
Fin width	54	34	32	25	24	20	18	14
Arm length								
Right I	35	23	16	15	15	13	[1]9	8
Right II	36	24	19	17	15	14	11.5	9
Right III	39	23	20	17	16	16	12	10
Right IV	46	28	22	20	15	15	13	11
Left IV	46	28	21	19	15	15	—	—
Arm hooks/suckers								
Right I	26/41	20/48	21/—	19/30	17/22	14/18	[1]15/16	11/19
Right II	27/32	23/38	22/—	16/20	18/18	18/18	17/18	14/14
Right III	28/36	21/28	22/—	22/22	17/15	20/18	18/16	14/21
Right IV	31/15	21/10	23/—	25/9	21/15	21/21	19/—	22/20
Left IV	31/22	28/38	25/—	26/16	21/18	21/12+	19/—	—
Tentacles right/left								
Tentacle length	—/86	61/—	65/68	43/—	51/46	48/51	42/42	23/27
Club length	—/20	15/—	15/15	12/—	11/11	11/11	9/9	7/7
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	—-7/7	7/7-—	6/7-6/7	7/6-—	7/7-6/7	—-7/6	7/7-—	6/6-5/7
Club suckers right/left								
Distal suckers	—/68	64/—	72/52+	70	64/72	—/64	72/—	68/64
Carpal suckers	—/4	4/—	3/4	4/—	3/4	—/4	3/—	4/4

[1] Length or count of left arm.

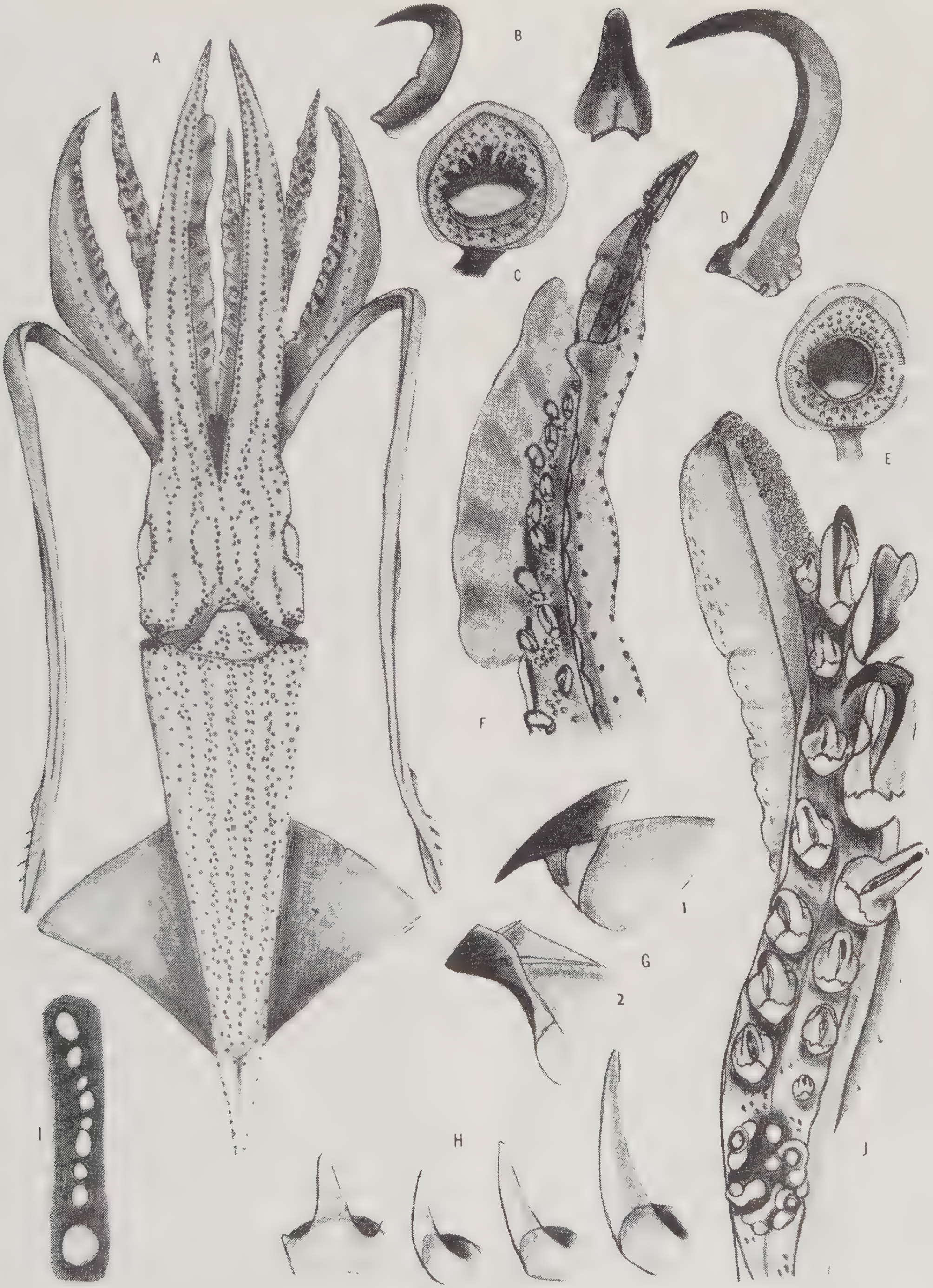


FIGURE 4.—*Enoploteuthis jonesi*. (A-F, I, and J from male holotype, ML (mantle length) 47 m; other body parts are from specimens as listed.) A, Ventral aspect; B, Dorsal arm hook, oral and lateral aspects; C, Dorsal arm sucker; D, Tentacular hook; E, Tentacular sucker; F, Hectocotylus; G, Mandibles: upper (1), lower (2), ML 27 mm; H, Radular teeth, ML 27 mm; I, Eye light organs; J, Tentacular club.

IV, 50.0-*55.0*-59.6). Arm IV is longest in both sexes. The arms are nearly square in cross section and they taper distally into fine delicate tips. The keels of arms I and II are confined mainly to the distal halves of the arms. The swimming keel of arm III is as wide as the arm at its midpoint. The lateral membrane (or tentacular sheath) of arm IV is moderately wide and extends to the tip of the arm. Dorsal and ventral protective membranes are present in all the arms. The ventral membrane is more developed than the dorsal, particularly on arm III.

In the males the right arm IV is hectocotylized. The ventral protective membrane on this arm forms a very wide lappet that extends from about the middle half, opposite the sixth pair of hooks, to about four-fifths of the arm length. Distally the membrane is much narrower and tapers to the arm tip (Fig. 4F). The dorsal protective membrane is slightly modified: a small tongue-like flap is developed opposite the distal end of the larger medial lappet. In addition, the males have numerous conical tubercles at the bases of the oral surface of all the arms and between the bases of all the hooks.

The biserial and regularly arranged hooks are completely sheathed by membranes (Fig. 4B). The distal arm suckers have long stalks. Each inner ring has eight teeth on its distal half and none on the smooth proximal half (Fig. 4C). The outer rings bear pegs all around. The suckers are progressively smaller distally; the distal suckers assume a globular shape, have small apertures, no teeth, and no outer rings.

The tentacles are longer than the mantle (TLI 104.9-*153.3*-188.9) and are about twice the length of the longest arm. The stalk is oblong in cross section near the base, very muscular, and almost as thick as arm III. The proximal part of the club is as narrow as the stalk or only slightly expanded. The club becomes unusually narrow in the distal one-third (Fig. 4J). The tip is blunt. The aboral keel is about one-half of the club length. A semilunar membrane is present on the ventral or oral side; it extends between the carpal area and the fourth pair of hooks. Protective membranes are developed on the ventral side but are rudimentary dorsally. Protective membranes are absent on the dactylus. The carpal cluster consists of three or four smooth-ringed suckers and several rounded pads in a compact round cluster together with some irregular grooves and ridges. There are 13 or 14 robust hooks in two rows on the club. The ventral row includes a series of greatly enlarged hooks. The hooks (Fig. 4D) are enclosed by membranes but the tips are exposed. These hooks have very broad bases and are set in rounded shallow excavations. Marginal suckers are absent. Twelve to 18 transverse rows of 4 small suckers per row occupy the narrow dactylus. About 12 of these suckers at the tip are slightly larger than the immediately preceding transverse row, thus forming a cluster at the tip of the club. All the club suckers have smooth inner rings (Fig. 4E). The pegs on the outer ring are moderately long and may hide the smooth edge of the inner ring from view.

The integumentary photophores occur in different sizes ranging from about 0.2 to 0.4 mm. A photophore may appear dark or very pale, depending on the extent of pigmentation. Many of the larger photophores are heavily pigmented, except for a small central area. Most of the smaller photophores are pale because pigmentation is confined to the periphery in the form of a very thin dark ring. Intermediate conditions between these extremes occur. At first glance the photophores on the mantle appear scattered at random, but on closer examination one can recognize four multiserial, ill-defined rows: two rows on each side of a very narrow midline space that extends from the anterior opening of the mantle to the tail and bounded laterally by a broad zone of photophores (Fig. 4A). Each row consists of large and small photophores set near each other; smaller and whiter ones occupy the central part of the row, while the larger and more conspicuously darker ones are located mostly on the outer area of the row. These rows become more difficult to distinguish posteriorly. A single row of evenly spaced photophores extends along the lateral margins of the tail. Numerous photophores occupy the ventrolateral surface and some single photophores, generally small ones, are scattered on the dorsal surface of the mantle, except near the midline. The edge of the mantle is lined by a single row of photophores; the photophores are spaced progressively farther apart toward the dorsal midline.

The funnel has six groups of photophores: Two rows separated by a midline space on the ventral side; a short row on each lateral side; and two dorsal rows, one on each side of the bridle.

A small triangular cluster of photophores is situated in the apex of the funnel groove. A space in the ventral midline of the head is broken by a short row of two or three photophores that bifurcates at the fork of the ventral arms; each branch continues along the ventral aboral side of arm IV to almost the tip. A row of closely set photophores runs along the edge of the funnel groove and divides near the apex of the groove into two branches, each with photophores in single file. The branches reunite near the base of arm IV. The row continues distally along the base of the tentacular sheath to the tip of the arm. The third lateral row on the head begins anterior to the first nuchal fold, has a gap at the window of the eye, and then continues and splits into two branches: A medial branch that continues anteriorly and ends near the base of arm IV at the midline of the tentacular sheath and a lateral branch that extends along the edge of the tentacular sheath and terminates about the level of the last hook on arm IV. The lateralmost row on the head also starts at the first nuchal fold, continues along the nuchal crest, and turns toward the posterior eyelid where it runs along the ventral edge to the optic sinus. The row begins again on the dorsal edge of the optic sinus, continues along the base of the swimming keel of arm III, and stops at about three-fifths of the arm length. The dorsal eyelid lacks photophores.

There are nine irregularly spaced photophores on the ventral part of the eyeball (Fig. 4I). The posteriormost light organ is larger than the anteriormost which in turn is larger than the remaining seven light organs. The latter are slightly different from each other in size and shape.

The teeth of the radula are long (lateralmost teeth are longest), blunt, and slightly curved (Fig. 4H). Of the seven teeth only the rachidian tooth has small lateral cusps.

The upper mandible of a small specimen (ML 30 mm) has distinct growth lines on the wings (Fig. $4G_1$). The riblike ridges on the gular plate of the lower mandible are well developed (Fig. $4G_2$).

The gladius is feather-shaped. The rachis is blunt anteriorly and forms a strong ridge dorsally through its length. The vanes are narrow, widest at about a third of the length of the gladius. The posterior end is curved inward ending in the cone.

The largest female (ML 82 mm) is gravid; the ovaries are distended and extend to the posterior part of the mantle cavity. The eggs are opaque and about 1 mm in diameter.

None of the males have spermatophores.

Young individuals: Immature individuals (ML 11-22 mm) have relatively wider mantles (MWI 45.5-*57.0*-72.7) than adults. At ML 11 mm the arms have the following armature: 1 to 3 suckers proximally, 7 to 12 hooks, and 15 to 20 suckers distally. The tentacles are distinctly longer than the mantle (TLI 172.7). The club has three hooks along with nine biserial suckers on the manus. Two of the suckers are slightly set apart (future carpal suckers). Four rows of minute suckers are located on the dactylus. At ML 17 mm the arms have no proximal suckers, 12 to 18 hooks, and 19 to 21 distal suckers. The club resembles that of the adult, except that two marginal suckers are present on the dorsal distal side of the manus and although there are already four carpal suckers, the carpus is still not completely developed. The photophores on the mantle are not distinctly arranged into rows, except for two medialmost rows which are separated by a narrow space (Fig. 2D). The rows on the head are each composed of photophores in single file (Fig. 2F). The number and position of the rows agree with those of the adult.

Remarks: Adults of this species resemble superficially *E. chuni* Ishikawa 1914 from Japan, but they are easily distinguished by the photophore pattern of the head and arms. *Enoploteuthis chuni* has seven rows of photophores on the head (including the rows passing along the ventral eyelids) (pl. XX, fig. 1, Sasaki 1920), whereas *jonesi* has six rows. There is a distinct midventral multiserial row on the head of *chuni*, whereas the ventral midline of *jonesi* is a clear space, except for two or three single photophores near the fork of the ventral arms anteriorly. Some rows of photophores on the head divide and reunite in *jonesi*, a condition absent in *chuni*. The row of photophores at the base of the swimming keel of arm III reaches the tip of the arm in *chuni*, but in *jonesi*, the same row ends slightly beyond one-half to three-fifths of the arm length. These observations were confirmed by T. Okutani of the Tokai Regional Research Laboratory (presently with the National Science Museum, Tokyo) who kindly examined specimens of *E. chuni* from Suruga Bay and compared them with illustrations of *E. jonesi* sent to him. In addition, there are more distal club suckers in *chuni* (90) than in *jonesi* (64-72) and these suckers are toothed in *chuni* and smooth in *jonesi*.

The counts and measurement of *E. jonesi* overlap those of *E. anapsis* Roper, 1964 from the tropical Atlantic and Caribbean. These species exhibit the following differences: 1) The midline space on the mantle in *jonesi* continues uninterrupted to the tail, but this space in *anapsis* has some scattered photophores near the tail; 2) the row that traverses the window on the ventral side of the head is bifurcate in *jonesi* whereas it is single in *anapsis*. The tentacles and clubs of *anapsis* are relatively longer than those of *jonesi*. The distal club suckers are more numerous in *jonesi* (64-72) than in *anapsis* (40-50).

This species is named after Everet C. Jones, former fishery biologist at the Honolulu Laboratory. It was under the supervision of E. C. Jones that the specimens collected during some of the cruises reached me in good condition.

Distribution: Central Pacific, Hawaiian waters, and equatorial region.

Enoploteuthis higginsi n. sp.
(Figs. 5, 2E, G; Table 4)

Enoploteuthis species B, Young 1978: figure 9B.

Holotype: Male, ML 37 mm, *Teritu*, Stn. 6 off Waianae, Oahu, September 1969, 110 m, USNM 729710.

Paratypes: 1 male, ML 35 mm, CHG-89, Stn. 11, 06°04.9′S, 157°36.9′W, 2 February 1966, 140-200 m, USNM 729714. 1 female, ML 53 mm, TC-32, Stn. 22, 21°02′N, 158°29.7′W, 21 July 1967, 67-117 m, USNM 729723. 1 female, ML 45 mm, TC-32, Stn. 56, 21°22.4′N, 158° 14.6′W, 23 August 1967, 97-179 m, USNM 577609.

Other material: 1 specimen, ML 27 mm, HMS-47, Stn. 51, 00°44′S, 149°46′W, 2 November 1958, 576 m. 1 specimen, ML 12 mm, CHG-51, Stn. 164, 16°44′N, 169°16′W, 14 February 1961, 100 m. 1 specimen, ML 12 mm, CHG-51, Stn. 172, 19°21′N, 169°20′W, 15 February 1961, 0-100 m. 1 specimen, ML 16 mm, CHG-89, Stn. 29, 04°05′S, 167°51′W, 14 February 1966, 120-135 m. 1 specimen, ML 11 mm, CHG-89, Stn. 30, 02°59′S, 167°51′W, 15 February 1966, 100-125 m. 1 male, ML 46 mm, TC-32, Stn. 23, 21°00.2′N, 158°30.1′W, 22 July 1967, 17-25 m. 1 female, ML 60+ mm, TC-32, Stn. 28, 20°58.6′N, 158°33.7′W, 25 July 1967, 8-60 m. 1 female, ML 30 mm, 2 specimens, ML 12 and 19 mm, TC-32, Stn. 33, 20°58.8′N, 158° 28.4′W, 13 August 1967, 83-99 m. 1 female, ML 32 mm, 1 specimen, ML 22 mm, TC-32, Stn. 37, 20°59.1′N, 158°12.7′W, 15 August 1967, 55-123 m. 1 male, ML 30 mm, 2 females, 37 and 40 mm, TC-32, Stn. 38, 20°58.7′N, 158°27.9′W, 15

TABLE 4.—Measurements (in millimeters) and counts of *Enoploteuthis higginsi*. TC = RV *Townsend Cromwell*; CHG = RV *Charles H. Gilbert*; + = missing mantle tip and lost suckers.

Cruise:	TC-32	TC-32	TC-32	TC-32	*Teritu*	CHG-89	TC-32	CHG-51
Station:	28	22	23	56	6	11	56	172
Sex:	Female	Female	Male	Female	(Holotype) Male	Male	Female	?
Mantle length	60+	53	46	45	37	35	29	22
Mantle width	24	20	18	14	14	13	13	11
Head width	20	17	13	14	15	12	11	10
Fin length	—	39	30	34	27	23	20	15
Fin width	58	42	38	34	30	30	24	21
Arm length								
Right I	42	32	25	26	20	20	[1]13	15
Right II	24	36	27	25	20	21	[1]15	12
Right III	48	33	28	28	21	20	[1]15	12
Right IV	51	37	28	31	23	23	19	11
Left IV	53	34	32	33	23	—	17	13
Arm hooks/suckers								
Right I	26/22	25/34	19/—	25/22	20/16	24/16	16/19	16/20
Right II	29/27	26/34	22/—	25/20	22/16	23/20	17/20	18/20
Right III	32/28	28/33	22/—	25/22	22/20	22/20	18/23	16/21
Right IV	28/28	26/21	25/—	29/20	22/2+	26/14+	22/23	18/6
Left IV	28/26	27/20	27/—	29/22	26/16	—	20/23	20/7
Tentacles right/left								
Tentacle length	—	108/117	110/—	—/92	41/41	60/—	—/48	34/27
Club length	—	17/17	16/—	—/16	11/11	11.5/—	—/9	—
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	—	5/6-5/6	4/6-—	—-6/6	5/6-5/6	5/6-—	—-4/6	—
Club suckers right/left								
Distal suckers	—	68/68	—	—/60	60/60	72/—	—/64	—
Carpal suckers	—	3/3	3/—	—/3	3/2	3/—	—/3	—

[1] Length or count of left arm.

August 1967, 8-25 m. 1 male, ML 46 mm, TC-32, Stn. 41, 20°58.9′N, 158°29.1′W, 16 August 1967, 59-122 m. 1 female, ML 37 mm, TC-32, Stn. 44, 21°00.1′N, 158°29.1′W, 18 August 1967, 72-118 m. 1 female, ML 47 mm, TC-32, Stn. 45, 20°58.1′N, 158°28.7′W, 18 August 1967, 12-31 m. 2 specimens, ML 27 and 28 mm, TC-32, Stn. 46, 20°57.6′N, 158°28.7′W, 18 August 1967, 77-118 m. 1 female, ML 35 mm, TC-32, Stn. 48, 20°59.7′N, 158°27.7′W, 19 August 1967, 60-104 m. 1 female, ML 29 mm, TC-32, Stn. 56, 21°22.4′N, 158°14.6′W, 23 August 1967, 97-179 m.

Description: The muscular mantle is slender (MWI 31.1-*37.9*-44.8) and conical; the translucent tail is slender and ends bluntly. The ventral anterior edge of the mantle is not deeply excavated and the lateral angles are pointed, but low. The dorsal anterior lobe is low.

The fins are triangular, wide (FWI 75.6-*81.2*-85.7), and long (FLI 65.2-*70.4*-75.6). The anterior margin near its attachment is a rounded lobe, but more laterally it appears straight. The lateral angles (about 75°) are rounded at the tip. The slightly concave posterior margins join the mantle independently, but the union of both fins (close to the tip of the mantle) is indistinct.

The funnel is triangular and wide at the base. The funnel valve is a wide semicircular flap. The funnel organ is large; an anterior papilla and thick lateral ridges are present. The funnel-mantle locking cartilage is simple with a shallow groove. The anterior part of the cartilage is slightly narrower than the posterior end.

The head is as wide as the mantle (HWI 28.3-*34.0*-40.5). The eye opening is a wide oval with a deep anterior sinus. The funnel groove is moderately deep and the lateral sides continue posteriorly as sharp ridges. The ventral ocular "windows" are translucent. The three nuchal folds are very prominent. The tongue-shaped olfactory organ is attached to the first fold closest to the funnel. The second and third folds are united to each other posteriorly and the third fold on each side continues as a much reduced fold toward the dorsal midline.

The buccal membrane has a DDVD attachment to the arms. Numerous folds and broad tonguelike papillae occur on the inner surface of the membrane. The external surface is densely supplied with small purplish chromatophores so that it is darker than most parts of the body.

The arms are slender but muscular, nearly square in cross section at the base and finely pointed at their tips. The arms are moderate in length (ALI: I, 44.8-*54.8*-60.4; II, 51.7-*58.0*-67.9; III, 51.7-*58.5*-62.3; IV, 58.6-*65.5*-73.3). Arm IV is longest in both sexes. The swimming keels are developed to about one-half of arm I distally, two-thirds of arm II distally, and complete in arm III where they are as wide as the arm at the midsection. The lateral membrane (tentacular sheath) of arm IV is wide and reaches to the tip of the arm. Dorsal and ventral protective membranes are developed on all the arms of both sexes. They are widest on arm III and least developed on arm IV, except on the hectocotylized arm of the male.

The right ventral arm of the male is hectocotylized. The protective membranes of this arm are modified. At about the middle half of the arm opposite the sixth pair of hooks, the ventral protective membrane becomes enlarged into a wide undulating flap that is reduced abruptly about three-fourths of the arm length and continues distally to the tip of the arm as a much narrower membrane. The dorsal protective membrane, on the contrary, is only slightly modified. A short semilunar flap is present opposite the distal end of the larger ventral flap (Fig. 5F). Numerous conical papillae are scattered on the oral surface of the arms of males between the bases of the hooks and on the bases of the arms.

The arms have biserial hooks proximally and biserial suckers distally. The hooks (Fig. 5E) are strongly attached and completely enclosed by sheaths. About half of the suckers at the tips of the arms have long stalks and wide openings. The distal half of the inner rim of the sucker has seven to eight teeth; the two middle teeth are narrower than the lateral teeth; a shelf is visible on the proximal half (Fig. 5B). The outer ring bears numerous pegs. The remaining suckers gradually become smaller distally, assuming a globular shape with smaller openings that lack teeth and outer rings.

The robust tentacles are much longer than the mantle (TLI 110.8-*190.3*-239.1). The stalk near the base is almost square in cross section and as stout as arm III. The carpus and manus of the club are wide but the dactylus is quite narrow (Fig. 5G). The carpal cluster is compact and it includes three smooth-ringed suckers (very rarely two suckers) and several rounded pads and some elongate ridges and grooves; these are arranged in an oval cluster. Ten to 12 very robust, sheathed hooks are present in two rows

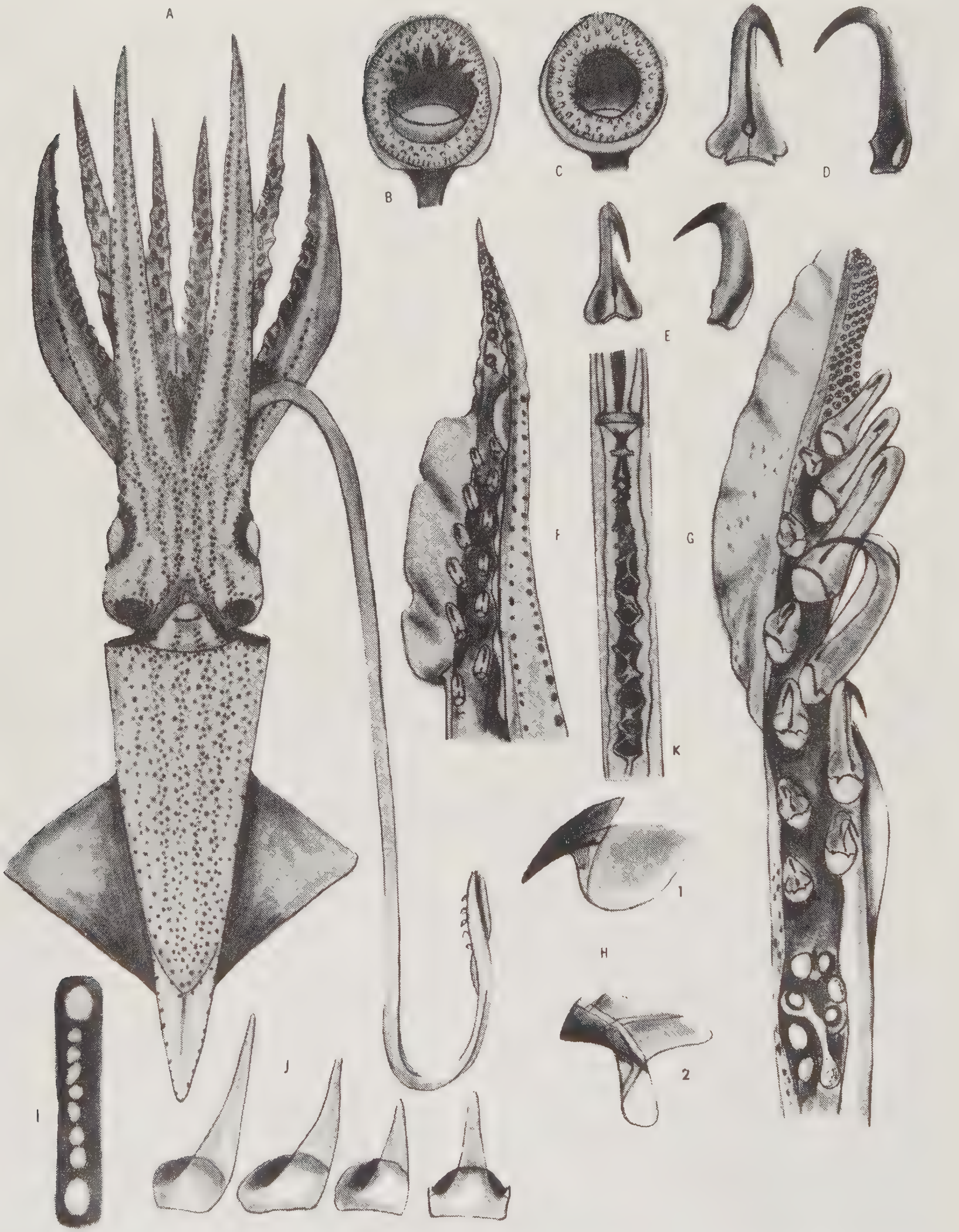


FIGURE 5.—*Enoploteuthis higginsi*. (A-E, G, and I from female paratype, ML (mantle length) 45 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Dorsal arm sucker; C, Tentacular sucker; D, Tentacular hook, oral and lateral aspects; E, Dorsal arm hook, oral and lateral aspects; F, Hectocotylus, male holotype, ML 37 mm; G, Tentacular club; H, Mandibles: upper (1), lower (2), female, ML 37 mm; I, Eye light organs; J, Radular teeth, female, ML 37 mm; K, Section of spermatophore, male, ML 46 mm.

on the manus. The ventral row includes a few large curved hooks, the largest hook is about one-fifth larger than the largest arm hook. The hooks have broad bases (Fig. 5D) and fit into shallow depressions on the club. The distal club suckers are arranged in four longitudinal rows (between 15 and 18 suckers in each row). The inner rings of these suckers are smooth but are surrounded by an outer ring with broad pegs that can be mistaken for teeth of the inner ring (Fig. 5C). A few suckers in the distal part of the dactylus are slightly enlarged and form a cluster there at the blunt end of the club. The dorsal or aboral keel is well developed and extends from opposite the third dorsal hook to the blunt end. A smaller semilunar membrane lies on the oral or ventral side of the club. It extends from opposite the distal half of the carpal cluster to opposite the second or third ventral hook. Protective membranes are poorly developed but recognizable.

The integumentary photophores range in size from about 0.2 mm to about 0.4 mm with varying degrees of pigmentation. Some are very dark with small pearl gray centers, others are lighter with varying widths of peripheral pigmentation. Those with very thin dark rings appear palest or almost white. The photophores on the ventral surface of the mantle appear to be distributed at random (Fig. 5A). They are concentrated on the ventral surface except at the tail and gradually become widely scattered toward the dorsal surface. A single row extends along each lateral margin of the tail. The free edge of the mantle opening is lined by a transverse row where the photophores are farther separated dorsally. There are no photophores on the fins, or on most of the ventral area of the tail.

Two rows of photophores separated by a median space are present on the ventral surface of the funnel. A shorter row or patch occurs on each of the lateral margins and a wider strip is found on each of the dorsolateral surfaces of the funnel.

The distribution of the photophores on the head is rather intricate. A small cluster lies in the apical region of the funnel groove. The ventral midline of the head is not totally clear of light organs, as a few isolated ones may be present. A very short row of three to four photophores in single file on the ventral midline (near the bases of arm IV) splits into two at the fork of the arms; each branch then continues along the ventral aboral edge of arm IV, ending a short distance from the distal tip of the arm. A row of photophores begins near the first nuchal fold, follows the curve of the funnel groove, and at a point near the apex of the funnel groove it splits into a wider medial branch and a narrower lateral branch. These branches reunite near the base of arm IV and the combined row proceeds anteriorly along the base of the tentacular sheath to the tip of arm IV. The next lateral row begins anterior to the first nuchal fold, is interrupted by a gap at the window of the eye, continues for a short distance, and divides into two short branches; each branch then extends to the edge of the tentacular sheath independently. A row of single photophores runs along the edge of the tentacular sheath and stops a short distance from the tip of arm IV. The lateralmost row on the head extends from the first nuchal fold along the nuchal crest, then anteriorly to and along the ventral margin of the eyelid, and ends at the ventral edge of the optic sinus. The row begins again on the dorsal edge of the optic sinus, continues along the base of the swimming keel of arm III, and terminates at about one-half the length of the arm. Two or three isolated small photophores occur in the area surrounding the ventral part of the eye opening; one photophore is usually located directly lateral to the window.

There are nine light organs on the ventral part of the eyeball. The terminal organs are much larger and slightly separated from seven smaller, closely set, light organs (Fig. 5I).

The radular teeth (seven teeth in a series) are long and slender. The outermost lateral teeth are longest while the innermost lateral teeth are shortest. The rachidian tooth has cusps. The three median teeth are almost straight while the two outermost lateral teeth are slightly curved (Fig. 5J).

The upper mandible (Fig. $5H_1$) has a pointed rostrum with very sharp edges and the lower mandible (Fig. $5H_2$) has three well-developed ribs on the gular plate.

The gladius is feather shaped and the midrib is low and rounded. The cone is narrow and rounded at the extreme end. The vanes start to broaden at about one-third of the length and reach their greatest width at about half of the length. The lateral edges of the gladius appear slightly thickened when held against a strong light.

Spermatophores from a male (ML 46 mm) are about 14 mm in total length. The cement body is slightly greater than half the length of the sperm reservoir and has two collars at the oral end (Fig.

5K), the anterior much smaller than the posterior. The aboral part of the spiral filament is supplied with numerous intricate diamond-shaped depressions separated by thickened ridges. Two to four turns are present behind the cap. A spermatophore examined has the following measurements:

Spermatophore segment	*Length (mm)*
Entire spermatophore	13.8
Sperm reservoir	5
Cement body	2.8
Spiral filament	6.0

Some eggs taken from the ovary of the female paratype (ML 53 mm) measured about 1.2 mm each.

Young individuals: Small individuals (ML 11-16 mm) have relatively wider mantles (MWI 56.3-*59.4*-63.6) and the photophores on the mantle are scattered (Fig. 2E) as they are in the adult. At ML 15 mm all the rows of photophores on the head correspond to those of the adult with respect to number and position (Fig. 2G). The most medial row consists of several photophores set close to each other as in the adult. All other rows are composed of a single line of photophores. At ML 12 mm the tentacles are robust and longer than the mantle (TLI 108.3), more than the length of the arm. The club has two carpal suckers, four hooks on the ventral side of the manus among a group of 16 suckers (presumably future hooks), some marginal suckers, and numerous quadriserially arranged suckers on the dactylus. The aboral keel is also developed. The arms bear between 12 and 14 hooks and a sucker at the base of one of the dorsal arms. Thirteen or 14 suckers occupy the distal part of arms I, II, and III, and 24 suckers on arm IV. At ML 16 mm there are still 4 club hooks and 2 carpal suckers, but the arm hooks have increased (18 on arm IV) as have the distal suckers. At ML 19 mm, 16 to 19 hooks are observed on the arms and 6 to 7 on the club along with an increased number of distal arm suckers and club suckers. At this stage three carpal suckers are present as in the adult.

Remarks: The species can be easily confused with *E. jonesi*; counts and measurements overlap and both species can be found in the same trawl hauls. However, a close examination of the material reveals a series of minor but consistent characteristics that separate one from the other even at a small size (ML 10 mm). At comparable sizes the tentacles and clubs are similar in structure, but *jonesi* has 13 or 14 club hooks and usually 4 carpal suckers while *higginsi* has 11 or 12 club hooks and usually 3 carpal suckers. Both have long tentacles, but they are relatively longer in *higginsi*.

Discrete longitudinal arrangement of photophores on the mantle is wanting in *higginsi* while a median space and identifiable rows are found in *jonesi*. The arrangement of photophores on the head also shows some differences: 1) The row closest to the midline is multiserial in *higginsi* whereas it is simple in *jonesi*; 2) isolated photophores occur in the midline area of the head and in the space near the eye in *higginsi* but are absent in *jonesi*; 3) the row directly anterior to the window is bifurcate in both species but in *higginsi* both branches extend to the tentacular sheath whereas in *jonesi* only the lateral branch does; and 4) the row of photophores on arm III is incomplete in both species, but in *higginsi* the row rarely extends more than 50% of the arm length (45-52% of arm length, 11 specimens) and in *jonesi* the row is more than half the arm length (56-85% of arm length, 18 specimens).

Enoploteuthis higginsi, like *E. jonesi*, shares many characteristics with *E. chuni* and *E. anapsis* (see remarks section of *E. jonesi*), but the scattered distribution of photophores on the mantle is distinctive of *higginsi*. Rows do not occur on the mantle in any stage of development in *higginsi*. At ML 10 mm, or smaller, the rows are already evident in *anapsis* (Roper 1966, figs. 22, 23).

Specimens captured in Hawaiian waters which were labeled *Enoploteuthis* sp. B and reported in Young (1978) also belong to this species (R. E. Young[3]).

This enoploteuthid squid is named after Bruce E. Higgins, former fishery biologist at the Honolulu Laboratory under whose leadership most of the material was collected during cruise 32 of the RV *Townsend Cromwell* in Hawaiian waters.

Distribution: Central Pacific, Hawaiian, and equatorial regions.

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[3] R. E. Young, Department of Oceanography, University of Hawaii, Honolulu, HI 96822, pers. commun. 3 March 1980.

Enoploteuthis reticulata Rancurel 1970
(Figs. 6, 2B; Table 5)

Enoploteuthis reticulata Rancurel 1970: figures 31-37 (incorrect spelling *reticula* in figures 31-33).

Enoploteuthis sp. (No. 1), Okutani, 1974: figures 12a, b, e.

Enoploteuthis sp. A, Young 1978: figures 9B, 10A.

Material examined: 1 male, ML 130 mm (regurgitated by a porpoise) CHG-7, 20°42.7′N, 157°50′W, 3 February 1953, USNM 729718. 1 male, ML 117 mm, HMS-30, Stn. 3, 28°38.5′N, 161°20.3′W, 16 July 1955, 100 m. 1 specimen, ML 26 mm, TC-7, Stn. 5, off Waianae, Oahu, 12 August 1964, 60-100 m. 1 female, ML 35 mm, TC-32, Stn. 3, 21°22.5′N, 158°13.5′W, 13 July 1967, 15-25 m. 1 specimen, ML 13 mm, TC-32, Stn. 4, 21°20.9′N, 158°13.1′W, 13 July 1967, 75-107 m. 1 specimen, ML 18 mm, TC-32, Stn. 6, 21°21.7′N, 158°13.3′W, 14 July 1967, 83-124 m. 1 female, ML 45 mm, TC-32, Stn. 9, 21°21.5′N, 158°13.5′W, 15 July 1967, 17-25 M. 2 females, ML 39 and 62 mm, TC-32, Stn. 15, 21°20.3′N, 158°12.2′W, 17 July 1967, 16-30 m, USNM 729691. 1 specimen, ML 30 mm, TC-32, Stn. 28, 20°58.6′N, 158°33.7′W, 25 July 1967, 92-122 m. 1 male, ML 46 mm, TC-32, Stn. 29, 20°59.5′N, 158°31.5′W, 26 July 1967, 8-60 m. 1 male, ML 71 mm, TC-32, Stn. 31, 20°59.6′N, 158°29.3′W, 13 August 1967, 80-121 m, USNM 577606. 1 specimen, ML 32 mm, TC-32, Stn. 46, 20°57.6′N, 158°28.7′W, 18 August 1967, 77-118 m. 1 male, ML 50 mm, TC-32, Stn. 48, 20°59.7′N, 158°27.7′W, 19 August 1967, 60-104 m.

Description: The mantle is almost circular in cross section and is very muscular; the tail is thin and translucent. The mantle is widest at the opening (MWI 27.4-*32.3*-37.1) and the sides converge gradually toward the saccate tail. The anterior ventral margin is very slightly excavated and the lateral angles are pointed, but low. The dorsal evagination of the mantle is a rounded and low lobe.

The fins are about three-fifths of the mantle length (FLI 62.4-*64.7*-67.7) and are moderately wide (FWI 59.8-*69.3*-82.6). They arise at about the anterior third of the mantle length. The anterior margin projects as a rounded lobe near its attachment and then extends laterally, and together with the almost straight posterior margin, a rounded angle (about 72°) is formed. The posterior margins are each joined to the mantle separately leaving a small gap between them.

The funnel is triangular and almost as wide as

TABLE 5.—Measurements (in millimeters) and counts of *Enoploteuthis reticulata.* CHG = RV *Charles H. Gilbert;* HMS = RV *Hugh M. Smith;* TC = RV *Townsend Cromwell;* + = missing arm tips and lost suckers.

Cruise:	CHG-7	HMS-30	TC-32	TC-32	TC-32	TC-32	TC-7	TC-32
Station:		3	31	15	29	28	5	6
Sex:	Male	Male	Male	Female	Male	?	?	?
Mantle length	130	117	71	62	46	30	26	18
Mantle width	38	32	22	23	17	12	11	10
Head width	31	30	19	17	13	12	8	8
Fin length	88	73	43	42	30	16	15	9
Fin width	85	70	48	44	38	20	18	14
Arm length								
Right I	65	58	[1]45	35	28	17	15	12
Right II	65	65	[1]46	43+	30	19	15	13
Right III	70	[1]60	[1]47	34+	30	18	16	12
Right IV	69	65	45	38	33	18	17	13
Left IV	72	66	48	40	31	19	17	13
Arm hooks/suckers								
Right I	26/—	24/8+	[1]21/24	21/20	20/15	20/11	21/14	21/14
Right II	24/—	24/19	[1]23/24	26/16	20/18	18/10	21/12	20/15
Right III	24/—	24/22+	[1]24/15	24/14	22/13	20/11	22/11	21/14
Right IV	32/—	34/17	33/20	28/11	29/9	27/12	30/9	30/10
Left IV	31/—	33/19	33/35	31/12	26/13	27/12	28/10	30/9
Tentacles right/left								
Tentacle length	120/126	93/115	76/68	80/60	47/49	22/28	20/20	—/16
Club length	20/20	21/21	16/16	—/14	14/14	8/8	6/6.5	—/5
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	5/5-4/5	5/6-5/6	6/6-7/5	5/5-5/5	5/6-4/5	5/5-5/5	4/5-5/5	—-3/5
Club suckers right/left								
Distal suckers	—	10/8	10/8	—	11/8	8/—	10/9	—/8+
Carpal suckers	5/4	4/6	6/6	5/5	5/5	4/6	5/7	—/6

[1] Length or count of left arm.

it is long. The funnel-mantle locking cartilage is simple. The anterior end is slightly pointed and narrower than the posterior end. The groove is shallow and wider posteriorly. The funnel organ has a papilla on the anterior end of the dorsal component (inverted V-shape), is small, and has wide ridges on the lateral limbs. The ventral components are oval but have pointed anterior ends. The funnel valve is broad and its rounded anterior edge reaches the level of the funnel opening.

The head is almost square in cross section, slightly rounded at the top, and narrower than the mantle (HWI 23.8-*26.4*-28.3). The ventral excavation is moderately deep and well marked by sharp lateral edges. The three nuchal folds on each side of the head are very prominent. The first nuchal fold bears a tonguelike olfactory papilla at its posterior end. The second and third folds are crescentic folds with broad anterior ends and are united to each other posteriorly by a narrow membrane. From the posterior end of the third fold a narrow membranous ridge extends toward the dorsal midline but does not quite reach it. In large specimens the nuchal crest connects the three folds to each other and to the midline, so that three oval areas are formed on each side of the head posteriorly. The eye opening is wide and has a deep sinus. Both dorsal and ventral ocular "windows" are easy to recognize, particularly in specimens that have been preserved longer.

The buccal membrane has eight stout supports with connectives attached to the arms in the order DDVD. The lappets are pointed and the inner surface of the buccal membrane is rugose and lacks papillae. The membrane is darker than the supports; small chromatophores are present in both structures.

The arms are moderate in length; the ventral arms, which are longest, are shorter than the mantle length (ALI: I, 49.7-*56.1*-63.4; II, 50.0-*58.9*-65.2; III, 51.3-*59.1*-66.2; IV, 53.1-*61.7*-71.7). Weak keels extend along the distal third of arm I, along the distal half of arm II, and from the base to the tip of arm III. In the largest specimen the swimming keel of arm III is slightly wider than the arm width. The tentacular sheath along arm IV is narrow, about half of the arm width near the base, and reaches the tips of the arms. The protective membranes are developed on borders of all arms, but are more strongly developed on the ventral borders. This is particularly so on arm III, although the ventral membrane is never wider than the height of the hooks. The trabeculae and the membranes are very distinct even at the tips of the arms.

The right ventral arm of the male is hectocotylized (Fig. 6B). The ventral protective membrane on this arm is enlarged into an undulating lappet, which extends from near the 9th or 10th pair of hooks to the arm tip, although it becomes progressively reduced in width distally. The membrane is deeply notched at about two-thirds of its length so that two semilunar flaps of unequal lengths are formed. The dorsal protective membrane is less developed than the ventral protective membrane even in the area opposite the enlarged lappet. In addition, the males have numerous conical tubercles distributed on the oral surface, at the bases of all the arms, and on the areas between the bases of the hooks.

The arm hooks are large (Fig. 6E), arranged in two alternate rows, and enclosed by sheaths. The ventral arms of both sexes bear the most hooks. None of the hooks are unusually enlarged or reduced in either sex. The distal part of each arm has two rows of suckers. The proximal suckers in this region have long stalks and the inner rings of these suckers have seven or eight large blunt teeth (middle two teeth broadest) distally and smooth proximally (Fig. 6C). The outer ring has long pegs. The most distal pairs of suckers (with about three teeth) are much reduced in size, carried on short stalks, and have small openings.

The tentacles are generally about the length of the mantle (TLI 79.5-*100.4*-129.0). The stalk is slender, only about one-third of the width of arm III. The sides are compressed and the cross section is almost triangular. The club is narrow (Fig. 6I). The carpus includes between four and seven smooth-ringed suckers and corresponding pads arranged in an elongated series which is limited on both sides by a narrow ridge. The manus includes a dorsal row of four to seven sheathed hooks and a ventral row of five or six slightly larger hooks. The hooks (Fig. 6F) have narrow bases. The largest hooks are not bigger than any of the largest arm hooks. Marginal suckers are absent and any sucker present along the rows of hooks in young specimens certainly represents an undeveloped hook. The dactylus has 8 to 11 suckers arranged in two rows. They have long stalks and wide openings. The sucker rings bear teeth; six or seven short teeth distally and six or seven very blunt teeth proximally (Fig. 6D). The outer ring has many short pegs. The tip of the club is blunt with a short over-

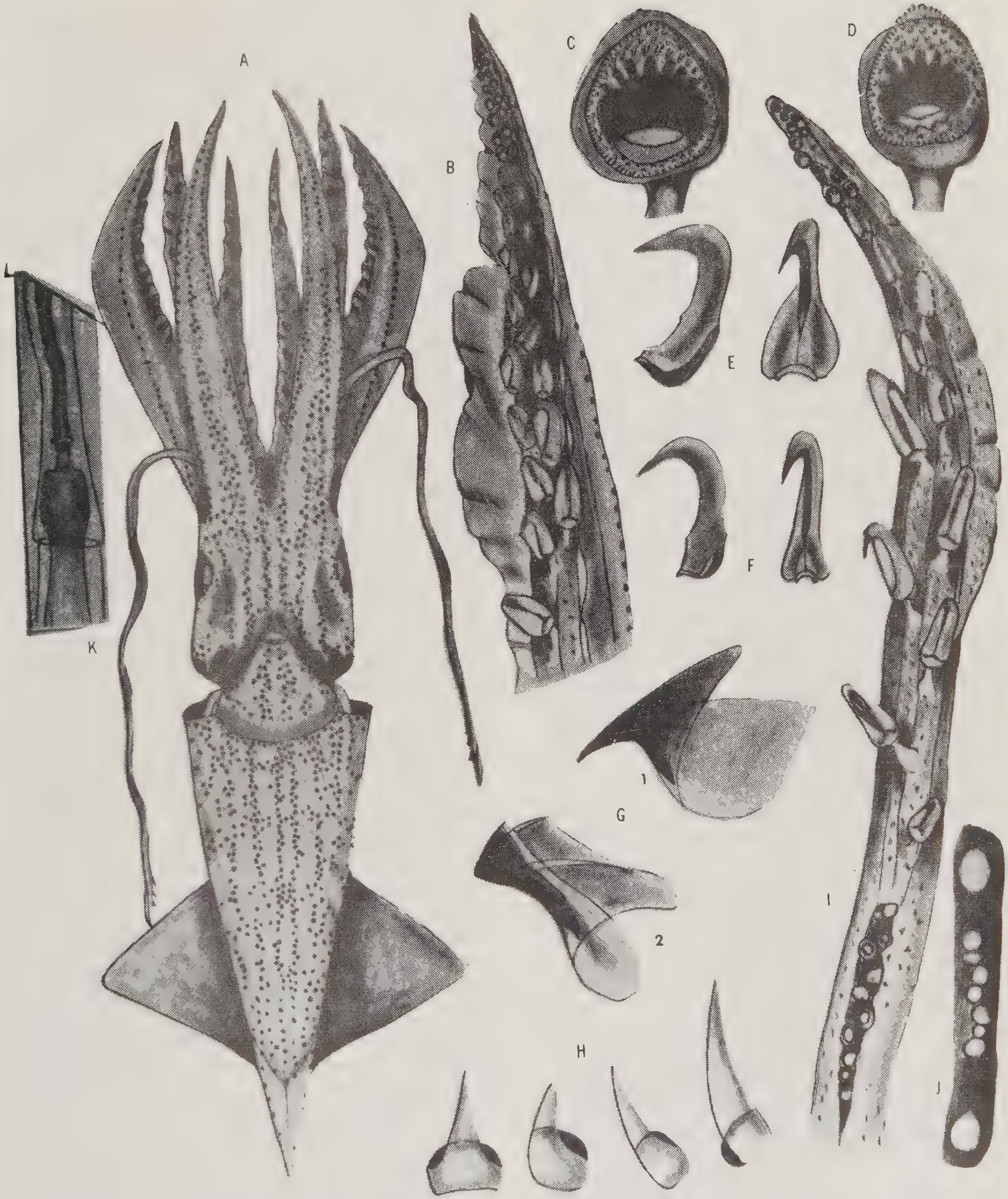

FIGURE 6.—*Enoploteuthis reticulata* Rancurel. (A, C-F, and J from female, ML (mantle length) 62 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Hectocotylus, male, ML 71 mm; C, Dorsal arm sucker; D, Tentacular sucker; E, Dorsal arm hook, oral and lateral aspects; F, Tentacular hook, oral and lateral aspects; G, Mandibles: upper (1), lower (2), male, ML 50 mm; H, Radular teeth, male, ML 50 mm; I, Tentacular club, male, ML 117 mm; J, Eye light organs; K, Section of spermatophore, male, ML 117 mm.

lapping hood which conceals a few of the suckers at the tip. The aboral keel is also narrow and extends from opposite the second hook to the lateral side of the hooded tip. Protective membranes are not developed on either side.

The photophores range in size from 0.2 to 0.4 mm. The dark or light appearance of each photophore is caused by the extent of pigmentation. The majority of the small ones are white owing to pigmentation confined only to the periphery of the photophores. The photophore pattern of the mantle is distinctive. It can be described briefly as the combined effect of about six ill-defined longitudinal rows and four oblique rows to produce a netlike or reticulated pattern (Fig. 6A). The photophores are scattered irregularly in the posterior region of the mantle, except on the tail where a single row extends on each side to the tip of the tail. The ventral area of the saccate tail lacks photophores. A single transverse row in which the photophores are farther apart dorsally lies along the anterior edge of the mantle. A few small photophores are distributed on the dorsal surface of the mantle. The fins lack photophores.

Two longitudinal rows, separated by a midline space, occur on the ventral surface of the funnel. A short row (connected to the ventral row posteriorly) is located on each side of the funnel and a long row of photophores is found on the dorsolateral side, close to each bridle.

The photophore pattern on the ventral side of the head is observed best in smaller specimens. Two clusters, separated by a narrow midline space, lie in the apex of the funnel groove. A clear space occupies the ventral midline of the head. Eight main rows of photophores (four rows on each side of the midline space) are present. The first or most medial row begins at the posterior end of the funnel groove, extends anteriorly to the ventral aboral side of arm IV, and reaches almost to the tip of this arm. The second row branches out from the first row near the apex of the funnel groove, extends parallel to the first row and joins it at a point near the base of arm IV, at about the same level as the anterior margin of the eye. At the base of arm IV the width of the second row is increased by additional photophores, and as the row continues along the base of the tentacular sheath distally it is gradually reduced to a single series of photophores which reaches the tip of the arm. A very short row or cluster of photophores occurs between the first and second rows at a short distance beyond the base of arm IV, but in older individuals this short row tends to lie closer to the second row and may be difficult to distinguish. The third lateral row extends from opposite the first nuchal fold anteriorly (interrupted by a gap at the window of the eye) to the base of arm IV where it merges with the second row. A branch continues further along the edge of the tentacular sheath almost to the tip of arm IV. The fourth or most lateral row extends from the second nuchal fold to the posterior margin of the eye and passes along the edge of the ventral eyelid to the ventral edge of the optic sinus. The row begins again on the dorsal edge of the optic sinus and continues along the base of the swimming keel of arm III to a short distance from the tip. An arclike row of small white photophores, spaced widely, lies along the ventral region of the eye between the third and fourth rows of photophores.

Nine light organs, arranged in a single row, are present on the ventral side of the eyeball. The terminal organs are much larger than the seven, closely spaced, interior light organs and are set apart from them. The interior organs are not of uniform size (Fig. 6J).

The seven radular teeth are blunt and slightly curved. The rachidian has low lateral cusps (Fig. 6H).

The mandibles are strong; the rostrum of the upper mandible is pointed and the edges are sharp (Fig. $6G_1$). The gular plate of the lower mandible is reinforced by three stout ribs (Fig. $6G_2$). At ML 45 mm the wings of both halves are already well pigmented.

The gladius is thin with a low rounded midrib. The vanes are narrow and widest at about the middle. The cone is thin-walled and as wide and rounded as the anterior end of the gladius.

The spermatophores are large. The cement gland has a large swelling at the aboral end (Fig. 6K). The aboral end of the spiral filament, anterior to the cement gland, is plain except for some longitudinal ridges. Two or three spiral turns behind the cap are present. Measurements from two specimens are given below:

Spermatophore segment	*Length (mm)* ML 130 mm specimen	*Length (mm)* ML 71 mm specimen
Entire spermatophore	28	14
Spiral filament	12	6.2
Cement gland	3	1.8
Sperm reservoir	13	6

Young individuals: At ML 13 mm the photophores on the mantle are arranged as small clusters of large photophores distributed in a definite pattern (Fig. 2Ba). There are a few small and large photophores on the head, arms, and funnel, and they are aligned in areas that correspond to the adult pattern. At this stage there are 17 to 21 arm hooks and 7 to 11 distal arm suckers. The tentacles are shorter than the mantle (TLI 84.6) and weak. On the club a single hook, along with 16 suckers in two rows, is developed; however, the carpal area is not yet differentiated. At ML 18 mm, 20 or 21 hooks and 14 or 15 distal suckers are present on each of arms I, II, and III, and 30 hooks and 9 distal suckers are present on arm IV. On the club, 6 carpal suckers are set apart from 8 hooks (biserial) on the manus and about 13 suckers on the dactylus. At ML 26 mm the photophore pattern of the mantle appears more complex. First, additional photophores develop between the clusters whereby four oblique rows are present; and second, six longitudinal rows of indistinct small white photophores are present (Fig. 2Bb). This pattern, although not as complicated, resembles that of the adult. At this stage the clubs have 9 or 10 hooks, 9 or 10 distal suckers (biserial), and 5 to 7 carpal suckers. A ML 45 mm female has an oviducal gland 2.0 mm long, and at ML 46 mm the right ventral arm of the male is already hectocotylized, although the lappet is still very narrow and the tubercles on the arm bases are minute. There is no indication of spermatophores in the still undeveloped genital system. However, a ML 50 mm specimen has spermatophores.

Remarks: The present material can be assigned with confidence to *E. reticulata* (Rancurel 1970). The photophore patterns of the mantle, head, and arms, and characteristics of the tentacles and clubs are very close, and hook counts (arms and clubs) overlap. Differences in measurements are not considered to be significant.

Okutani (1974; 51, fig. 12a, b, e) described and illustrated a specimen, labeled n. sp. (No. 1) in his paper on the cephalopods collected at lat. 17°53′S, long. 126°18′W during the EASTROPAC Expedition, 1967-68; I have examined this particular specimen deposited in the U.S. National Museum; it is *E. reticulata.*

Enoploteuthis sp. A of Young (1978) belongs to *E. reticulata* described here (R. E. Young footnote 3).

The reticulated pattern is not unique. A similar pattern has been described for *E. galaxias* Berry, 1918. However, these two species differ in a number of basic features. Except for the mantle photophores, the pattern of the light organs in *galaxias* is unlike that of *reticulata*; there is a median row present in the head of *galaxias* flanked by three lateral rows, or a total of seven rows. A median row is absent in *reticulata.* I have examined the type of *E. galaxias* deposited at the Australian Museum, Sydney, Australia. Unfortunately, the specimen has darkened considerably and the photophore pattern is no longer recognizable with an ordinary microscope. The tentacles and clubs are very different. The tentacular stalk in *galaxias* is as stout as the arms, but in *reticulata* the stalk is only a third of the arm width. The club of *galaxias* has an expanded carpus, whereas in *reticulata* the carpus is very slender. The carpal suckers and pads in *galaxias* are arranged in a compact oval area, but in *reticulata* they are biserially arranged lengthwise in a narrow area. The suckers of the dactylus in *galaxias* are quadriserially arranged and quite numerous (38-43), whereas they are biserially arranged and very few (8-11) in *reticulata.* Lastly, the rachidian tooth of *galaxias* has no cusps, but that of *reticulata* does.

The present collection data and those from the literature show that *E. reticulata* occurs over a wide area of the Pacific, Hawaiian waters included, from lat. 28°38.5′N to 22°58′S and from long. 164°04′E to 126°18′W.

GENERAL DISCUSSION

Since the description of *Loligo leptura* by Leach (1817) and the subsequent designation of this species as the type of the genus *Enoploteuthis* Orbigny, 1848 by Pfeffer (1900), only five other valid species have been described: *E. chuni* Ishikawa 1914; *E. galaxias* Berry 1918; *E. anapsis* Roper 1964; *E. theragrae* Taki 1964; and *E. reticulata* Rancurel 1970. (See summary of history, synonymy, and generic diagnosis in Roper 1966.)

Enoploteuthis dubia Adam 1960 was described from a single specimen captured in the Gulf of Aqaba, Red Sea. However, Adam in his remarks was not certain that it was an *Enoploteuthis.* With more material and information several years later, he removed the species from *Enoploteuthis* (Adam 1973).

Enoploteuthis theragrae was described from seven specimens found in the stomach contents of two codfish, *Theragra chalcogramma*, captured in 1957 and 1962 from two localities in the Japan Sea. These specimens probably are allied to *E. chuni*. Except for the mantle photophores (six in rows for *theragrae* and eight in rows for *chuni*) all other diagnostic characters are shared by both species (M. Okiyama[4]).

GEOGRAPHIC DISTRIBUTION

Enoploteuthis anapsis and *E. leptura* are widely distributed in the Atlantic. *Enoploteuthis leptura* is known from the Gulf of Guinea (type locality), Madeira, Cape Verde Islands, the southern Straits of Florida (Roper 1966), and east of Bermuda (Roper 1977). *Enoploteuthis anapsis* is recorded from parts of the western Atlantic in the Gulf of Mexico and Caribbean Sea, from the mid-Atlantic, Madeira, St. Helena, and South Equatorial Current (Roper 1966), and east of Bermuda (Roper 1977).

Enoploteuthis chuni was first described from Toyama Bay, Sea of Japan, and Sasaki (1920) reported it later, again from Toyama Bay and farther south from Bungo Strait. Shimomura and Fukataki (1957) recorded it again from the sea of Japan together with *Watasenia scintillans* in the stomach contents of Alaskan pollock. Okutani (1967) listed an adult specimen from Sagami Bay on the Pacific side of Japan and some larval stages later (1968), also from the Pacific side of Japan. The first and only record of *E. theragrae* is from the Sea of Japan in 1964.

Enoploteuthis galaxias is known only from the type locality, off Gabo Island to Everard Grounds, Victoria, Australia.

Enoploteuthis reticulata was described from specimens taken by midwater trawl and from stomach contents of *Alepisaurus ferox* caught in areas of the southwest Pacific, approximately between lat. 22° and 18°S and long. 164°E and 133°W. The present material extends the distribution to lat. 21°N in the Hawaiian area and Okutani's specimen (1974, *Enoploteuthis* sp. No. 1) to the southeast Pacific at lat. 17°S, long. 126°W.

The genus *Enoploteuthis* was first reported from the central Pacific by King and Ikehara (1956) in their study of the food and feeding habits of the yellowfin tuna and bigeye tuna. They found a total of 36 specimens of *Enoploteuthis* in the stomach contents of these fishes. There are no other previous records of the genus from the central Pacific. The station data of the present material show that *E. obliqua* ranges approximately from lat. 11°N to 5°S and long. 81° to 144°W; *E. octolineata* from lat. 7°N to 3°S and long. 144° to 157°W; *E. jonesi* from lat. 20°N to 14°S and long. 157° to 168°W; and *E. higginsi* from lat. 21°N to 4°S and long. 149° to 169°W. Of the five species found in the central Pacific, namely, *obliqua*, *octolineata*, *jonesi*, *higginsi*, and *reticulata*, the last three species range to areas close to the Hawaiian Islands whereas *obliqua* and *octolineata* do not (Fig. 7). Based on available records, *reticulata* has the widest range; it is found in the southwest Pacific, Hawaiian area, and southeast Pacific. Collections made between September 1969 and November 1974 by the University of Hawaii include specimens of *E. reticulata* and *E. higginsi* (Young 1978).

BATHYMETRIC DISTRIBUTION

The genus *Enoploteuthis* is rare in collections, and, except for *E. anapsis* (Roper 1966), *E. higginsi*, and *E. reticulata* (Young 1978), few depth records are available.

Useful depth data are available for only two specimens of *E. leptura* studied by Roper (1966). These specimens were taken from depths between 0 and 170-300 m. *Enoploteuthis anapsis* is represented by 25 specimens taken from depths between 33 and 600 m at night and a single specimen from very deep waters, 2,000 m, during the day. Roper and Young (1975) mentioned the capture of an *E. anapsis* specimen in a closing net at 90 m, off Bermuda at night.

Depth records are not included in the original description of *E. chuni*; however, the *Albatross* specimens reported by Sasaki (1920) came from the stomach of a fish captured from deep water, about 857 m. Okutani (1967, 1968) reported an adult from a depth of 700 m and two larval stages from the surface.

The only known specimens of *E. galaxias* (four specimens) were captured at depths between 288 and 450 m.

The present material, except for that from two tows at 240 and 576 m, came from depths between the surface and 179 m. Depth data and other pertinent records are listed in Table 6 for 131 specimens of *obliqua*, *octolineata*, *jonesi*,

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[4] M. Okiyama, Tokyo University, Tokyo, Japan, pers. commun. 26 November 1970.

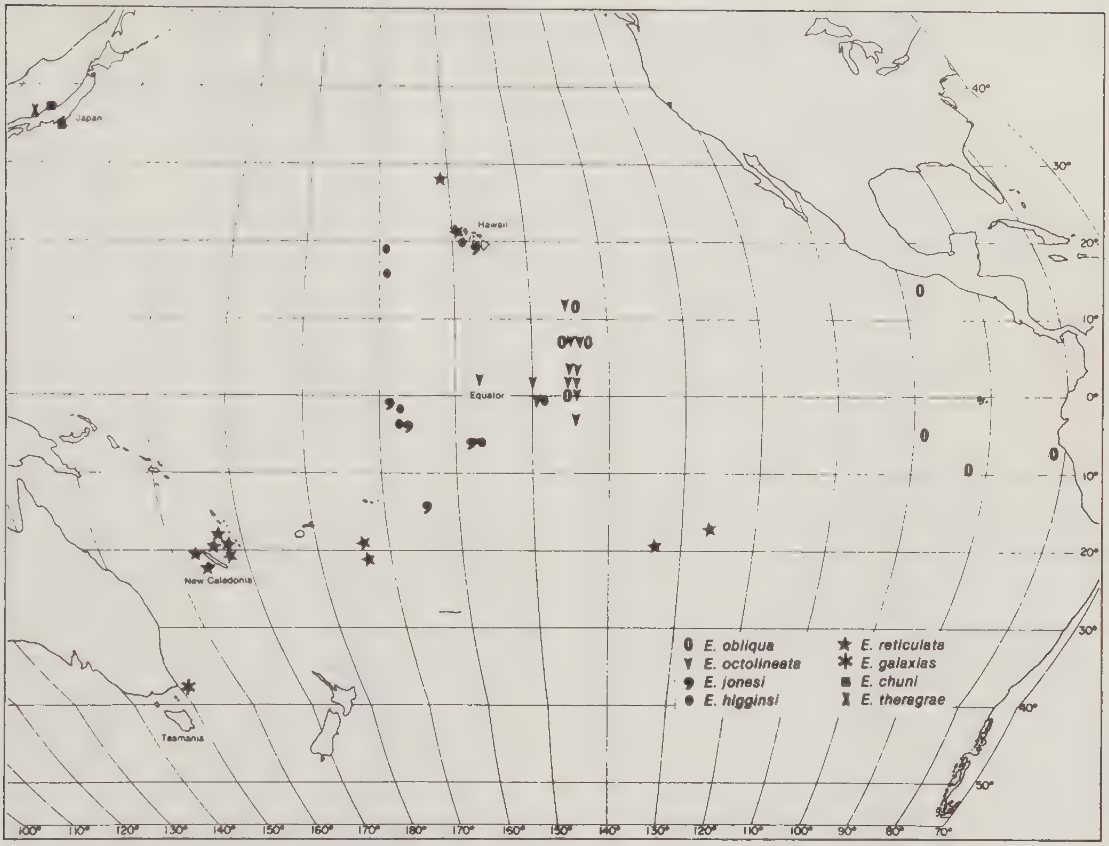
Japan
Hawaii
Equator
New Caledonia
Tasmania
0 E. obliqua
▼ E. octolineata
E. jonesi
● E. higginsi
★ E. reticulata
✱ E. galaxias
■ E. chuni
E. theragrae
40°
30°
20°
10°
0°
10°
20°
30°
40°
50°
100°
110°
120°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80°
70°

FIGURE 7.—Distribution of *Enoploteuthis* species in the Pacific.

higginsi, and *reticulata*. Most of the specimens (93.1%) were taken between the surface and 150 m, and the greatest number of these (48.1%) came from a depth of 50 m. A majority of the specimens (70.2%) were collected at night between 1900 and 0400. A limited number of specimens (8.4%) came from the few tows made during the day. *Enoploteuthis higginsi* and *E. reticulata* captured off Oahu, Hawaii, were taken close to the surface (50-100 m) at night and much deeper (500-600 m) during the day (Young 1978).

Species of *Enoploteuthis* are undoubtedly mesopelagic forms (200-1,000 m day habitat) that make diel vertical migrations as has been demonstrated for *E. anapsis* by Roper (1966) and for two other *Enoploteuthis* by Young (1978).

RELATIONSHIPS

The Pacific species of *Enoploteuthis* fall into two natural groups allied either to *E. anapsis* or *E. leptura* along the same characters that separate these two Atlantic species (see Roper 1966). Apparently, there are two species complexes within the genus: Species that tend toward the development of larger clubs and long and muscular tentacles, and those species that exhibit the opposite trends.

Additional features of the former complex are: many suckers in four rows on the clubs, large hooks, and oval to round carpal apparatus. These are features common to *galaxias*, *chuni*, *theragrae*, *anapsis*, *jonesi*, and *higginsi*. Within this group, *anapsis*, *jonesi*, and *higginsi* all have the semilunar membrane on the club while *galaxias* and *theragae* are illustrated in the literature without it. Both Berry (1918) and Taki (1964) do not mention the semilunar membrane in their species descriptions. I have seen the holotype of *galaxias*, but I could not verify the presence of the membrane because of the poor

TABLE 6.—Bathymetric data of *Enoploteuthis* species: *obliqua, octolineata, jonesi, higginsi,* and *reticulata.* TC = RV *Townsend Cromwell*; HMS = RV *Hugh M. Smith*; CHG = RV *Charles H. Gilbert.*

Cruise no.	Station no.	No. of specimens	Mantle length (mm)	Sex	Depth (m)	Time 24 h	Month
Enoploteuthis obliqua							
TC-48	19	1	58	M	50	—	April
TC-48	11	1	55	M	50	—	March
TC-46	9	1	50	F	50	1945-0230	October
TC-44		[1]1	50	F	—	—	July-August
TC-46	9	1	41	M	50	1945-0230	October
TC-48	19	1	40+	F	50	—	April
TC-44	24	1	37+	M	50	1933-0245	July
TC-44	17	[1]1	27	—	—	—	July
TC-44	24	4	12-20	—	50	1933-0245	July
TC-43	14	16	5-18	—	50	1945-0235	May
TC-43	22	5	12-17	—	50	2017-0237	May
TC-43	10	5	12-17	—	50	1943-0239	May
TC-44	18	2	12-17	—	100	1947-0253	July
TC-44	32	1	13	—	50	1937-0303	July
TC-44	54	1	12	—	50	1932-0238	July
TC-47	16	4	6-11	—	50	1930-0250	January
TC-48	16	3	7-10	—	20	—	April
TC-44	16	2	55-10	—	0	1059-0129	July
Enoploteuthis octolineata							
TC-43	52	1	75	F	50	1940-0244	May
HMS-47	58	1	71	F	212	2013-2153	November
TC-46	47	1	56	F	115	1939-0240	October
TC-46	37	1	56	F	50	1934-0236	October
TC-48	50	1	49	F	50	—	April
TC-48	52	1	46	M	50	—	April
TC-43	42	2	21-40	—	50	1942-0235	May
TC-48	35	1	39	—	50	—	April
TC-46	41	1	36	—	50	1935-0230	October
TC-48	92	1	33	—	50	—	April
TC-43	38	3	19-30	—	50	1944-0240	May
TC-44	44	1	28	—	—	1935-0237	July
TC-44	26	1	26	—	20	1934-0243	July
TC-44	68	1	25	—	75	1932-0235	August
HMS-47	58	1	25	—	212	2013-2153	August
TC-43	48	1	24	—	50	1943-0240	May
TC-43	52	2	20-22	—	50	1940-0244	May
TC-43	26	1	20	—	50	1945-0235	May
TC-44	56	1	20	—	50	1933-0235	July
TC-47	45	2	16-20	—	50	2000-0200	February
TC-43	12	1	15	—	20	1945-0226	May
CHG-89	5	1	15	—	120-240	2058-2332	July
TC-46	45	2	14	—	50	1934-0234	October
HMS-47	51	1	10	—	576	2013-2158	November
Enoploteuthis jonesi							
TC-7	12	1	82	F	9-13	1926-2056	August
TC-7	12	1	47	M	9-13	1926-2056	August
TC-32	28	1	40	F	92-122	1952-0152	July
CHG-89	24	1	35	M	90-130	2053-2246	February
TG-32	46	1	35	F	77-118	1951-0151	August
TC-32	39	1	30	F	63-101	1053-0153	August
CHG-89	14	1	27	M	70-80	0258-0445	February
CHG-89	29	1	22	—	120-135	2038-2231	February
CHG-89	31	1	17	—	90-150	2040-2233	February
TC-32	37	1	11	—	55-123	0354-0954	August
Enoploteuthis higginsi							
TC-32	28	1	60+	F	8-60	1952-0152	July
TC-32	22	1	53	F	67-117	1952-0152	July
TC-32	45	1	47	F	12-31	1143-1743	August
TC-32	41	1	46	M	59-122	1151-1751	August
TC-32	23	1	46	M	17-25	0403-1003	July
TC-32	56	1	45	F	97-179	1952-0152	August
TC-32	38	2	37-40	F	8-25	1144-1744	August
TC-32	44	1	37	F	72-118	0353-0953	August
Teritu	6	1	37	M	110	—	September
TC-32	48	1	35	F	60-104	1155-1755	August
CHG-89	11	1	35	M	100-200	0254-0445	February
TC-32	37	1	32	F	55-123	0354-0954	August
TC-32	38	1	30	M	8-25	1144-1744	August
TC-32	33	1	30	F	83-99	1950-0150	August
TC-32	56	1	29	F	97-179	1952-0152	August
TC-32	46	2	27-28	—	77-118	1951-0151	August
HMS-47	51	1	27	—	576	2013-2153	November
TC-32	37	1	22	—	55-123	0354-0954	August
TC-32	33	2	12-19	—	83-99	1950-0150	August
CHG-89	29	1	16	—	120-135	2038-2231	February
CHG-51	164	1	12	—	0-100	2105-2323	February

TABLE 6.—*Continued.*

Cruise no.	Station no.	No. of specimens	Mantle length (mm)	Sex	Depth (m)	Time 24 h	Month
CHG-51	172	1	12	—	0-100	2100-2250	February
CHG-89	30	1	11	—	100-125	0603-0745	February
Enoploteuthis reticulata							
CHG-7		[2]1	130	M	—	daylight	February
HMS-30	3	1	117	M	100	2105-2315	July
TC-32	31	1	71	M	30-121	0354-0954	August
TC-32	15	1	62	F	16-30	0352-0952	July
TC-32	48	1	50	M	60-104	1155-1755	August
TC-32	29	1	46	M	8-60	0343-0755	July
TC-32	9	1	45	F	17-25	0354-0954	July
TC-32	15	1	39	F	16-30	0352-0952	July
TC-32	3	1	35	F	12-15	0355-0955	July
TC-32	46	1	32	—	77-118	1951-0151	August
TC-32	28	1	30	—	92-122	1952-0152	July
TC-7	5	1	26	—	60-100	2023-2156	August
TC-32	6	1	18	—	83-124	0354-0954	July
TC-32	4	1	13	—	75-107	1146-1747	July

[1] From stomach of *Alepisaurus*.
[2] Regurgitated by a porpoise.

condition of the specimen. *Enoploteuthis galaxias*, *chuni*, and *theragrae* have a midventral row of photophores on the head flanked by two lateral rows which extend (without branching) to the ventral arms. These three species are found in the western Pacific: *chuni* and *theragrae* from Japan and *galaxias* from Australia. The remaining species of this complex, *anapsis*, *jonesi*, and *higginsi*, are very similar: All have distal club sucker rings without teeth; all have an incomplete midventral row of photophores on the head (represented by a short anterior segment near the base of the ventral arms and by a triangular patch of photophores in the apex of the funnel groove); the first lateral row of photophores on the head is divided and reunited before extending to the ventral arms; and all have an incomplete photophore row on arm III. The longitudinal rows of photophores on the mantle are easily recognized in *anapsis* and *jonesi*, but not in *higginsi*.

Enoploteuthis leptura, *octolineata*, *obliqua*, and *reticulata* comprise the other species complex. They all have thin, slender, and short tentacles, clubs without semilunar membranes, few club suckers that lie in two rows, and a continuous midventral space on the head. *Enoploteuthis octolineata* and *E. leptura* are similar in that both have distinctly separated first and second lateral rows of photophores on the head, and lack a triangular patch of photophores in the apex of the funnel groove although each of the first lateral rows continues into the groove. Both species also have distinct and well-spaced mantle and funnel photophores. *Enoploteuthis reticulata* and *E. obliqua* also show similarities. The photophore pattern on the head, arms, and funnel have basically the same arrangement: Two small clusters of photophores, separated by a narrow space, are present in the apex of the funnel groove and, except for the continuous midventral space, single photophores are present posteriorly in the spaces between the funnel photophore rows. Thus, the rows are not completely separated. However, the mantle photophore pattern of each species is distinct: oblique in one and reticulate in the other. *Enoploteuthis reticulata* and *E. galaxias* have similar patterns of mantle photophores, but their head photophore patterns and some features of the clubs differ. The reticulate pattern on the mantle is probably an independently developed trait.

The spermatophores of *E. higginsi* and *E. anapsis* are both intricately sculptured, while those of *E. leptura*, *E. obliqua*, and *E. reticulata* are simple. Since the spermatophores of the other species are undescribed, it remains to be seen if the sculptured type are only associated with the first species complex and the simple type with the second complex. The important characters (except photophore pattern) of these two complexes are listed in Table 7.

KEY TO THE SPECIES OF *ENOPLOTEUTHIS* (ADULTS, WORLDWIDE)

1. Tentacular stalk and club narrow, suckers on dactylus few and in two rows; carpal cluster elongate; semilunar membrane absent 2

TABLE 7.—Some comparative features of *Enoploteuthis anapsis* and *E. leptura* complexes. ML = mantle length.

Species	Maximum ML (mm) Female	Maximum ML (mm) Male	Tentacle length index	Club length index	Carpal suckers	Shape of carpus	Club hooks No.	Club suckers No.	Club suckers arrangement	Club sucker ring teeth No.	Semi-lunar membrane
anapsis complex											
chuni	87	63	119.0-147.0	21.6-25.4	4-6	polygonal, oval	9	90	quadriserial	5-8	present
galaxias	87	73	102.6-108.3	25.6-26.4	4-6	round, oval	11	38-43	quadriserial	undescribed	absent
theragrae	80	60	83.3-91 3	25.0	5	ellipsoid	10	many, minute	quadriserial	undescribed	absent
anapsis	76.9	54	163.0-275.7	29.1-47.1	3-4	rectangular	12-13	40-50	quadriserial	absent	present
jonesi	82	47	104.9-188.9	24.4-40.7	3-4	round	13-14	60-72	quadriserial	absent	present
higginsi	60+	46	110.8-239.1	29.7-36.1	2-3	oval	10-12	60-72	quadriserial	absent	present
leptura complex											
leptura	44.5	79	89.0-96.0	17.9-20.6	5-6	elongate	6-12	10-15	biserial	7	absent
obliqua	50	58	62.1-96.4	17.0-26.0	4-5	elongate	8-9	11-17	biserial	6-7	absent
reticulata	62	130	79.5-129.0	15.4-30.4	4-7	elongate	8-12	8-11	biserial	6-7	absent
octolineata	75	46	93.3-112.7	25.0-28.3	3-6	elongate	9-11	16-17	biserial	10	absent

1. Tentacular stalk and club robust, suckers on dactylus many and in four rows; carpal cluster round to oval; semilunar membrane present or absent 5

2. Mantle photophores in longitudinal rows only 3
2. Mantle photophores in longitudinal and/or oblique rows 4

3. Eight well-spaced mantle rows, all reaching anterior mantle edge; eight photophore rows on head, second and third lateral rows united posteriorly .... *octolineata*
3. Seven well-spaced mantle photophore rows, only six reaching anterior mantle edge; eight photophore rows on head, none united .... *leptura*

4. Two photophore rows on median part of mantle, oblique photophore rows on sides .... *obliqua*
4. Longitudinal rows and intersecting oblique rows of photophores on mantle (reticulate pattern) .... *reticulata*

5. Midventral photophore rows on head complete; first and second lateral photophore rows unbranched; photophore row on arm III complete 6
5. Midventral photophore row on head incomplete; first lateral photophore row on head divided and reunited; photophore row on arm III incomplete 8

6. Eight photophore rows on mantle, distinct for one-third of mantle length; semilunar club membrane present .... *chuni*
6. Six photophore rows on mantle or no rows, photophores scattered; semilunar club membrane absent 7

7. Six photophore rows on mantle, photophores scattered on posterior half of mantle......................... *theragrae*
7. No photophore rows on mantle, mantle photophores scattered; some areas devoid of photophores .... *galaxias*

8. Mantle photophores not in rows, photophores scattered .... *higginsi*
8. Six longitudinal photophore rows separated by narrow space................. 9

9. Midventral space not extending to tail, this space occupied by scattered photophores near tail .... *anapsis*
9. Midventral mantle space narrow, extending to tail .... *jonesi*

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DEVELOPMENTAL STAGES OF THREE CALIFORNIA SEA BASSES (*PARALABRAX*, PISCES, SERRANIDAE)

JOHN L. BUTLER, H. GEOFFREY MOSER,
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

GREGORY S. HAGEMAN, AND LAYNE E. NORDGREN
Department of Biological Sciences
University of Southern California
University Park
Los Angeles, California 90007

ABSTRACT

Eggs, larvae, and juveniles of kelp bass, *Paralabrax clathratus*, barred sand bass, *P. nebulifer*, and spotted sand bass, *P. maculatofasciatus*, are described from specimens reared in the laboratory and from specimens collected in the field. Eggs of spotted sand bass are 0.80-0.89 mm in diameter; eggs of kelp bass and barred sand bass are 0.94-0.97 mm in diameter. Larvae and juveniles of the three species may be distinguished by differences in pigmentation during most stages of development. Larvae of the two species of sand bass are indistinguishable during notochord flexion. Yolk-sac larvae of all three species are indistinguishable.

RESUMEN

Se describen los huevecillos, las larvas, y los juveniles de *Paralabrax clathratus, P. nebulifer*, y *P. maculatofasciatus*, tomadas de especímenes cultivados en el laboratorio y de especímenes recolectados en el mar. Los huevecillos de *P. maculatofasciatus* son de 0.80-0.89 mm de diámetro; los de *P. clathratus* y de *P. nebulifer* son de 0.94-0.97 mm de diámetro. Larvas y juveniles de las tres especies pueden ser distinguidos por las diferencias in pigmentación durante casi todos los estadios del desarrollo. Las larvas de *P. nebulifer* y *P. maculatofasciatus* no se pueden identificar durante la flexión del notocordio. Las larvas con saco vitelino no pueden separarse en las tres especies.

INTRODUCTION

Three species of the genus *Paralabrax* commonly occur off California. The kelp bass, *Paralabrax clathratus*, is found from Magdalena Bay, Baja California, to the Columbia River. The barred sand bass, *P. nebulifer*, is found from Magdalena Bay to Santa Cruz. The spotted sand bass, *P. maculatofasciatus*, is found from Mazatlan to Monterey (Miller and Lea 1972). A fourth species, the gold spotted bass, *P. auroguttatus*, has been reported on one occasion (Fitch and Schultz 1978). Prior to this record, the species was known from Cedros Island south to Cabo San Lucas and the Gulf of California (Fitch and Shultz 1978). Larvae of *Paralabrax* sp. have been illustrated by Kendall (1979) from CalCOFI specimens, which we have identified as *P. clathratus*. All three species are found in nearshore areas from the surface to about 600 feet (Miller and Lea 1972).

The kelp and sand basses combined rank second in the California sport fish catch (Oliphant 1979). Identifying these three species in ichthyoplankton collections may be important in monitoring population changes and assessing the impact of human activities on the nearshore environment. This paper describes the early life history of kelp bass, barred sand bass, and spotted sand bass from laboratory-reared and field-collected material.

METHODS

Eggs and larvae of *P. clathratus* were initially reared from artificially spawned eggs. Two ripe kelp bass, a 42-cm female and a 40-cm male, were caught by hook and line near Bird Rock, Santa Catalina Island, California, on June 22, 1978. Gonads were removed from the fish and taken to the laboratory, where eggs were collected into finger bowls. The eggs were flooded with seawater immediately before the introduction of several drops of sperm. The eggs and sperm were agitated for several seconds, followed by several changes of seawater. When the eggs hatched, a mixture of plankton and ground Tetramin was added as food. Although the larvae fed, they did not survive beyond yolk absorption.

Eggs and larvae of *P. clathratus, P. maculatofasciatus*, and *P. nebulifer* were reared from eggs collected off San Diego with plankton nets during May through September 1978 and 1979. For each collection a 60-cm, 505-mm mesh plankton net was towed at the surface for 15-20 minutes. Plankton was placed in 14-liter buckets filled with seawater. The samples were brought to the laboratory, and the fish eggs were sorted from the plankton. *Paralabrax clathratus* and *P. nebulifer* larvae were reared from eggs measuring 0.94-0.97 mm in diameter in several mixed cultures from June 1978 through 1979. Since eggs of two

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species were indistinguishable, developmental series were determined by working backwards from identified juveniles. On July 26, 1979, a large number of eggs measuring 0.82-0.86 mm were sorted from plankton collected off Mission Bay, California. This culture yielded only *P. maculatofasciatus* larvae and juveniles.

Larvae were reared to juveniles in a closed system on a diet of *Brachionus biplicata* and field-collected plankton. After about two weeks, the diet was gradually shifted to field-collected plankton supplemented with *Artemia* nauplii. Representative stages were photographed under anesthesia and preserved in 4 percent Formalin. A series of larvae was stained to study development of head spines. Additional material was obtained from the field collections of various institutions.

DEVELOPMENT

At 19°C, *P. clathratus* hatched at 36-40.5 hours after fertilization. Yolk-sac absorption was complete at 121.5 hours, or about 5 days. In larvae reared at 21°C from eggs collected in the plankton, notochord flexion began 11 days after hatching and was complete in some specimens on day 13. The earliest transformed juvenile was preserved 28 days after hatching.

Hatching time of *P. maculatofasciatus* is uncertain, since all eggs with the same diameter and size of oil globule regardless of stage of development made up the initial culture. All eggs hatched at 21.5°C within 24 hours after collection. Yolk-sac absorption was complete by day 4. Notochord flexion began on day 12 and was complete by day 19. The earliest transformed juvenile was preserved on day 28.

DESCRIPTION OF *PARALABRAX CLATHRATUS* AND *P. MACULATOFASCIATUS* EGGS

Eggs of both species are spherical in shape with clear, unsegmented yolk, a single large oil globule, and a clear, unsculptured chorion. Eggs of *P. clathratus* and *P. nebulifer* have a mean diameter of 0.95 mm, with a range from 0.94-0.97 mm ($n=25$). The mean diameter of the oil globule is 0.20 ($n=25$). Eggs of *P. maculatofasciatus* have a mean diameter of .84 with a range of 0.80-0.89 ($n=11$). The oil globule has a mean diameter of 0.17 with a range of 0.16-0.19 ($n=11$). Late-stage embryos of both species have similar pigmentation. At 24 hours, the embryo of *P. clathratus* is uniformly pigmented with small (0.1 mm) melanophores on the dorsal surface. Two to four melanophores are present on the oil globule, which lies midway between the head and tail of the embryo.

DESCRIPTION OF LARVAE AND JUVENILES

Paralabrax clathratus *(Girard 1854) Kelp Bass*

(Figures 1-4)

Distinguishing characters. Preflexion larvae may be distinguished from *P. nebulifer* by the number of the postanal melanophores, and from *P. maculatofasciatus* preflexion larvae by the position of those melanophores. The large ventral melanophore is on the eighth or ninth postanal myomere in *P. clathratus*. In preflexion *P. maculatofasciatus* the large ventral melanophore is on the sixth or seventh postanal myomere. Preflexion *P. nebulifer* have more small postanal, midventral melanophores, 11-20 ($\bar{x} = 14.5$), than *P. clathratus* 4-8 ($\bar{x} = 6.2$), or *P. maculatofasciatus*, 6-11 ($\bar{x} = 8.0$). The abdominal fin-fold pigment is heavier on *P. clathratus* than on the other two species. It forms a heavy broad triangle anterior to the anus. The postanal dorsal pigment patch is retained in *P. clathratus* until after 4.1 mm, but it is lost in *P. maculatofasciatus* by 3.4 mm. Larvae of *P. nebulifer* typically lack postanal dorsal pigment at all stages.

From early flexion (ca. 5.0 mm) through midflexion (ca. 5.9 mm), *P. clathratus* may be distinguished from the other two species by the large postanal pigment patch, the heavy preanal abdominal fin-fold pigment, and the lack of pigment on the lateral line. From late flexion through the end of the larval phase, *P. clathratus* may be distinguished by the presence of pigment on the upper jaw, the heavy pigment on the first dorsal fin, and the absence of pigment on the lateral line. Transformation to the juvenile stage takes place at about 11 mm. At this time vertical bars form on the body; they are quite different from the horizontal stripes of juvenile sand basses. Pigment anterior to each pectoral fin base forms a characteristic acute angle.

Description. Early yolk-sac larvae (Figure 1A) are fairly uniformly pigmented along the dorsal surface from the nape to the end of the tail. Pigment is also present over the oil globule. As the yolk is absorbed the dorsal pigment becomes concentrated into discrete patches. The first dorsal patches to become distinct are lateral to the midline and over the center of the yolk sac.

During the yolk-sac period, the dorsal pigment is concentrated into three areas: over the middle of the yolk sac, over the end of the gut, and midway between the anus and the end of the notochord (Figure 1B). Pigment is also present on the head anterior and dorsal to the unpigmented eyes. Pigment is present lateral to the gut in the region of the yolk sac and ventral to the gut posterior to the yolk sac, becoming heaviest near the anus. A ventral midline series of melanophores is

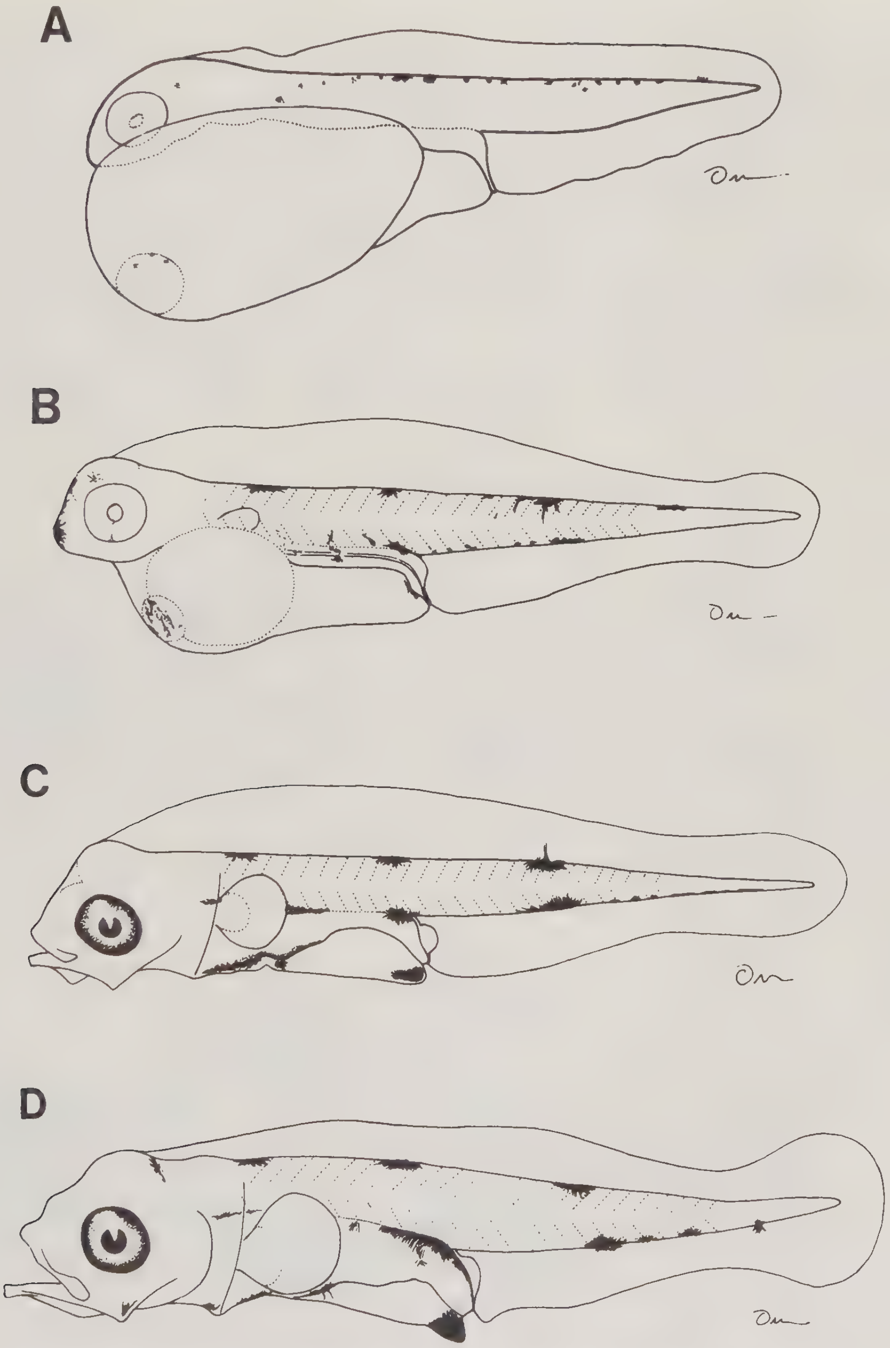

Figure 1. Larvae of *Paralabrax clathratus*: *A*. 2.2-mm yolk-sac larva, 1 day; *B*. 2.8-mm yolk-sac larva, 1 day; *C*. 3.0-mm preflexion larva, 4 days; *D*. 4.1-mm preflexion larva, 7 days.

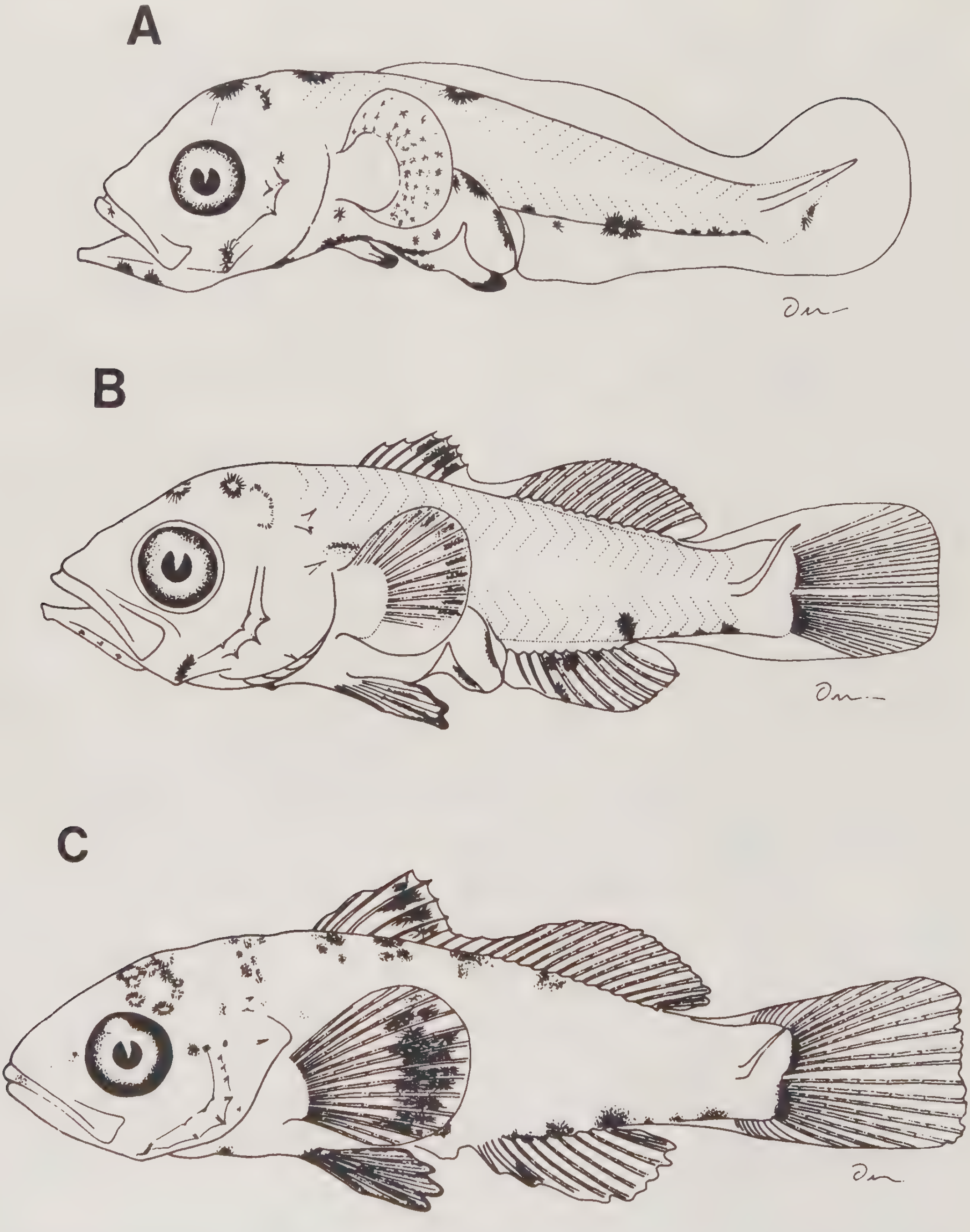

Figure 2. Larvae of *Paralabrax clathratus: A.* 5.1-mm flexion larva, 12 days; *B.* 7.4-mm postflexion larva, 25 days; *C.* 10.0-mm postflexion larva.

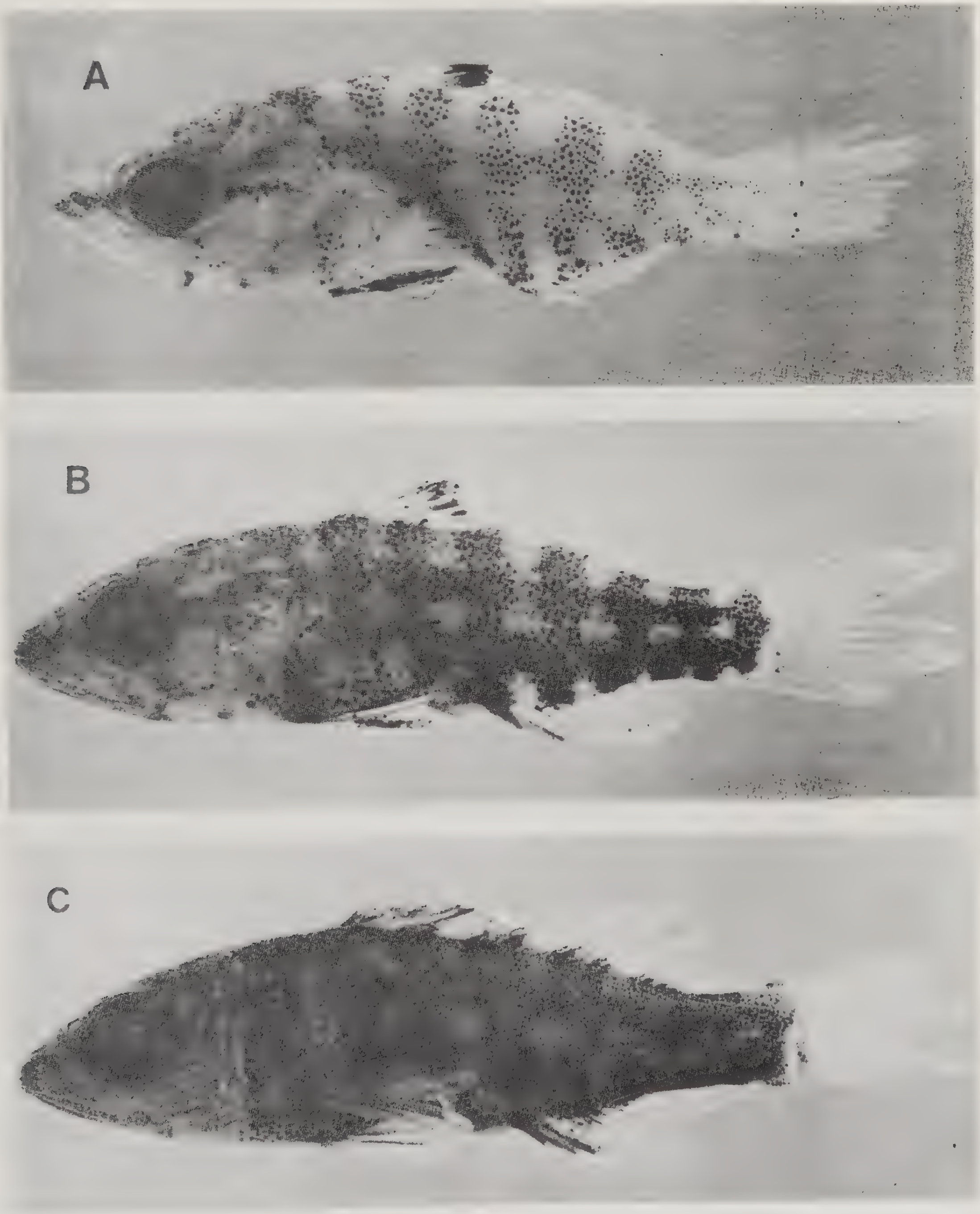

Figure 3. Developmental stages of *Paralabrax clathratus: A.* 11.1-mm transforming specimen, SIO 75-468; *B.* 11.2-mm transforming specimen, SIO 75-468; *C.* 16.6-mm newly transformed juvenile, SIO 75-468.

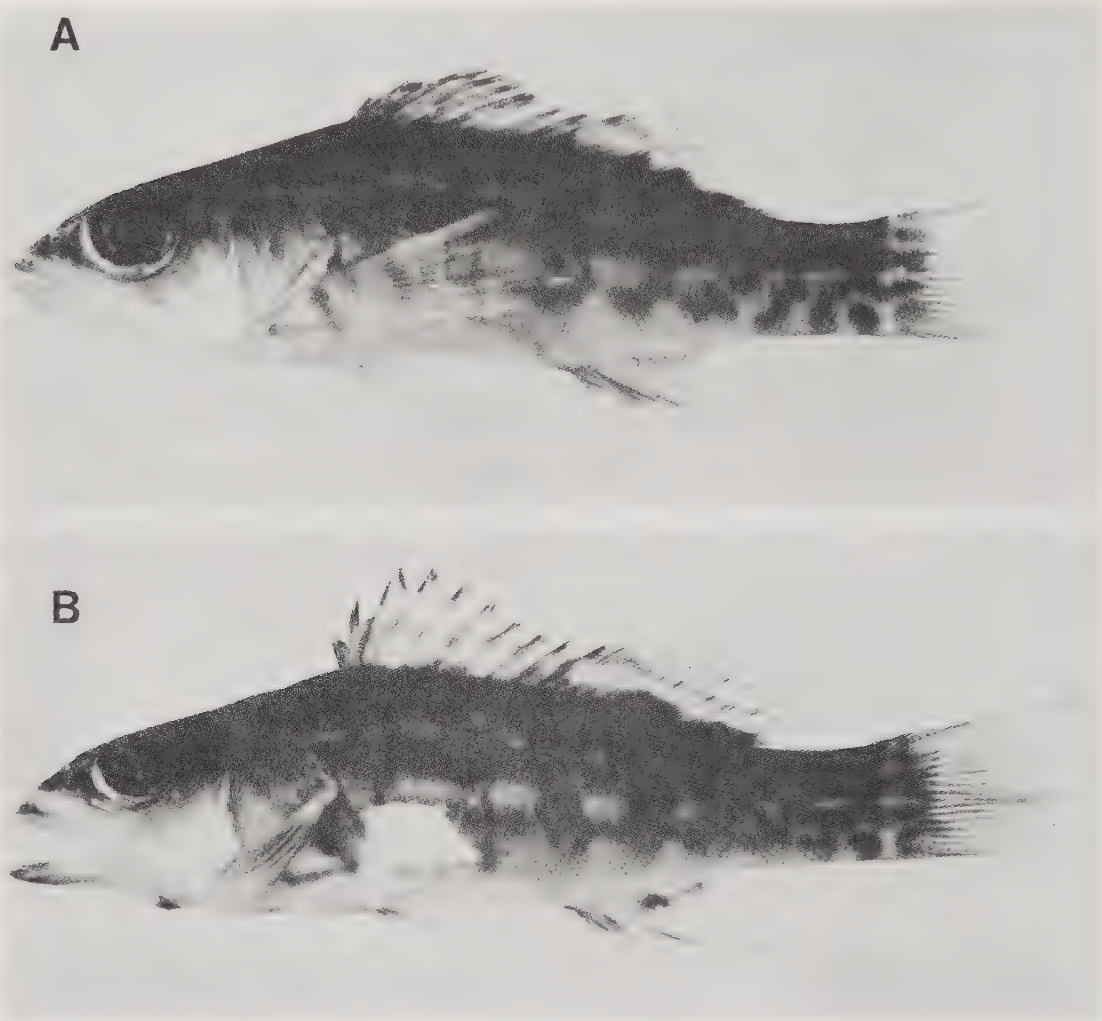

Figure 4. Juveniles of *Paralabrax clathratus*: *A*. 36.3-mm juvenile, SIO 73-345, Mission Bay, San Diego; *B*. 46-mm juvenile, SIO 73-345, Mission Bay, San Diego.

present from the end of the gut midway to the end of the tail, with heaviest concentration over the anus and midway to the end of the tail. The eyes become pigmented as the yolk is completely absorbed. Pigment on the snout and on the head is lost at this time. Dorsal pigment is concentrated into three large melanophores: midway between the snout and the anus, over the anus, and midway from the anus to the end of the notochord (Figure 1C). Pigment is present dorsal to the gut below the second dorsal midline melanophore at the point where the gut is deflected ventrally from the body. Pigment is present ventral to the gut from the junction of the cleithra posteriorly to the midpoint of the gut. A large, triangularly shaped pigment patch is present in the abdominal fin fold just anterior to the anus. A large ventral melanophore is present midway from the anus to the end of the tail, and a series of small melanophores continues posteriad almost to the end of the notochord.

This basic pigmentation pattern changes only slightly from yolk absorption at about 3.0 mm to just prior to caudal flexion (Figure 1D). Between 4.2 mm and 4.6 mm, the posteriormost dorsal pigment patch is lost. During this time pigment forms on the dorsal surface of the head and on the isthmus.

During notochord flexion (5.0-6.2 mm), the anal and pelvic fins form, and the abdominal fin fold is partially resorbed. Pigment forms on the pectoral fins and on the upper jaw (Figure 2A). The posteriormost ventral tail pigment becomes associated with the hypurals and, by the end of caudal flexion, forms a line at the posterior end of the hypural bones (Figure 2B). The large ventral tail spot lies at the posterior end of the forming anal fin (Figure 2B). Some of this pigment becomes internal when the fin is completely formed. The more anterior ventral pigment migrates onto the base of the anal fin. The dorsal midline melanophore located above the gut migrates onto the spinous dorsal fin, which forms at the end of flexion. The anterior dorsal midline melanophore either migrates to the head or is lost. It is absent in larvae larger than 6.9 mm. The characteristic triangular patch of pigment on the preanal abdominal fin fold becomes located on the ventral surface of the gut as the fin fold is resorbed (Figure 2B). The pelvic fins become heavily pigmented, particularly at their posterior margins. Pigment is absent over the lateral body surface.

Changes in postflexion larvae from about 7.4 mm to 10 or 11 mm are gradual. The most important pigment change is the addition of pigment on the snout and on the operculum behind the eye to form a prominent horizontal eye bar (Figure 2C). Reared larvae are heavily pigmented on the membranes of the spinous dorsal, pectoral, and pelvic fins, whereas pigmentation on field specimens is usually lighter in these areas. Postanal pigment coalesces along anterior rays, and dorsal pigment coalesces in discrete patches. In some field-collected larvae the vertical barring of the juveniles is faintly visible (Figure 2C).

The development of this striking pattern of vertical pigment bars is shown in the series of transforming individuals (Figure 3). A broad bar extends ventrad from the nape; three bars underlie the spinous dorsal fin; two extend between the soft dorsal fin and anal fin; one is at the caudal peduncle; and one overlies the hypural region. These are partially interrupted by two horizontal stripes: one is a continuation of the stripe through the eye and extends posteriad to the caudal fin base, and the other runs between the pectoral fin base and the caudal base. In larger juveniles the bars and stripes become obscured by the more prominent pattern of large, pale blotches (Figure 4). Juveniles of this stage have a characteristic angulate pigment blotch anterior to the pectoral fin.

The development of prominent vertical barring in early juveniles (Figure 4) may be rapid and associated with environmental stimuli. The juveniles are found under floating kelp where the disruptive coloration of the vertical bars would be cryptic. This type of coloration is also found in carangids and stromateoids that also associate with floating objects.

Kendall (1979) described the general morphology of *Paralabrax* larvae and made comparisons with other serranid genera. His material was not identified as to species, but his illustrations were of *P. clathratus*. We found the larvae of *P. clathratus* to be morphologically similar to the other two species studied (Tables 1 and 2). Ontogenetic trends of increasing snout-anus distance, head length, and body depth, relative to standard length, occur in all three species. Relative eye size decreases during the larval period in all three species and then increases in the juveniles. In *P. clathratus* and *P. nebulifer*, relative snout length reaches a maximum at notochord flexion and declines during later stages, whereas in *P. maculatofasciatus* the maximum is in postflexion larvae (Table 2). Relative snout length is greater in *P. clathratus* than in the other two species during all stages of development, and older larvae and early juveniles of *P. clathratus* have a more pointed snout than the other two species (Table 2).

Kendall (1979) described the complement of head spines for *Paralabrax* larvae (presumably *P. clathratus*), but did not give the sequence of development. The first spines to appear in *P. clathratus* are on the preopercle. At 4.7 mm a single preopercular spine is present in association with a single spine anterior to it on the preopercular ridge. Spines are added dorsally and ventrally to the initial spines to form anterior and posterior preopercular series. A maximum of three spines develops in the anterior series in postflexion larvae. These spines become obsolete at the end of the larval period and are absent in specimens larger than 11.0 mm. The posterior series contains a maximum of 6 spines at the end of the larval period and 7 in transition specimens. Spines continue to accrue on the upper region of the preopercular series in early juveniles, while the spines on the lower portion of the series are lost. Our largest stained specimen had 18 comb-like preopercular spines.

Upper and lower posttemporal spines appear first in a 5.9-mm specimen. The upper spine remains prominent throughout the larval period and is present in juveniles. The lower posttemporal spine disappears during the transitional stage after 10 mm SL.

The spine on the interopercle appears first in a 5.9-mm larva, remains throughout the larval and transitional stages, but is absent in most early juveniles. A subopercular spine was present on one 6.5-mm larva and two transitional specimens but was

TABLE 1
Measurements (mm) of *Paralabrax clathratus*

Age (days)	Body length	Snout to anus	Head length	Snout length	Eye	Body depth at P_2	Caudal peduncle depth	Caudal peduncle length
1	2.2	1.4						
1	2.7	1.4						
4	3.0	1.5	0.6	0.16	0.22	0.4		
2	3.1	1.6	—	—	—	—		
5	3.2	1.7	0.8	0.20	0.28	0.5		
5	3.4	1.8	0.7	0.16	0.30	0.5		
5	3.8	2.0	0.9	0.22	0.28	0.6		
5	3.8	2.1	1.0	0.24	0.28	0.6		
5	4.1	2.2	1.0	0.28	0.32	0.6		
7	4.1	2.2	1.0	0.28	0.32	0.6		
11	4.6	2.4	1.3	0.36	0.40	0.9		
12	5.0	2.8	1.6	0.5	0.5	1.2		
19	5.5	2.9	1.7	0.5	0.4	1.2		
25	5.9	3.3	2.1	0.6	0.6	1.6		
13	6.2	3.8	2.2	0.6	0.6	2.0		
25	6.8	3.9	2.5	0.7	0.7	1.8	0.6	1.2
25	7.3	4.4	2.7	0.7	0.7	2.2	0.8	1.2
—	8.3	5.0	3.0	1.0	0.9	2.4	1.1	1.4
—	8.9	5.2	3.1	0.7	0.8	2.7	1.2	1.4
—	9.2	5.2	3.2	0.8	0.8	2.7	1.2	1.5
—	9.8	5.7	3.6	1.1	1.0	2.8	1.3	1.5
28	10.0	5.8	3.6	0.9	1.0	3.1	1.4	1.7
—	10.3	6.3	4.1	1.1	1.0	3.1	1.3	1.7
—	10.5	6.4	4.1	1.1	1.2	3.0	1.3	1.8
—	10.7	6.4	4.2	1.1	1.2	3.0	1.4	1.8
—	11.3	6.7	4.6	1.2	1.2	3.2	1.5	1.8
—	12.0	7.2	4.7	1.2	1.2	3.6	1.5	1.9
—	12.3	7.5	4.8	1.3	1.2	3.8	1.5	1.9
—	13.0	7.8	5.2	1.7	1.3	3.7	1.7	2.2
—	13.5	8.3	5.2	1.3	1.3	3.7	1.6	2.1
—	14.0	8.8	5.7	1.7	1.3	4.5	1.8	2.2
—	14.2	8.7	5.8	1.5	1.5	4.0	1.8	2.2
—	15.6	9.3	6.2	1.7	1.3	4.6	2.1	2.5
—	15.8	9.3	5.8	1.3	1.7	4.7	2.0	2.6
—	18.2	11.0	6.4	1.5	1.7	5.5	2.6	2.9
—	21.0	12.8	8.0	1.7	2.0	6.4	3.0	3.1
—	23.0	14.0	8.5	2.3	2.2	6.8	3.2	3.5

Specimens between dashed lines are undergoing notochord flexion.

absent on all other specimens examined. The upper opercular spine appears at 6.5 mm and persists throughout development. The lower opercular spine is the last of the head spines to develop and is first evident on a 13.5-mm juvenile.

Development of head spines does not differ significantly among the three species studied. Each type of spine appears at about the same size in the three species, persists to a comparable stage of ontogenesis, and therefore is not helpful in species identification.

Paralabrax nebulifer *(Girard 1854) Barred Sand Bass* (Figures 5-7)

Distinguishing characters. Yolk-sac larvae of *P. nebulifer* were not distinguishable from *P. clathratus* or *P. maculatofasciatus*. Preflexion larvae may be distinguished from those of *P. clathratus* and *P. maculatofasciatus* by the large number, (11-20)$\bar{x} = 14.5$, of small ventral melanophores on the tail. The second dorsal midline melanophore is more anterior than in the other two species. In addition, most preflexion *P. nebulifer* larvae lack the posteriormost dorsal midline melanophore and have pigment on the horizontal septum. Flexion larvae of *P. nebulifer* may be distinguished from *P. clathratus* by the pigment along the horizontal septum; however, *P. nebulifer* appears to be indistinguishable from *P. maculatofasciatus* at this stage. In postflexion larvae of *P. nebulifer* (ca. 8.8 mm), pigment forms in a broad saddle under the first dorsal fin, rather than in several discrete saddles as found in *P. clathratus*. Similar sized *P. maculatofasciatus* are more heavily pigmented. Early juveniles (ca. 12-16 mm) of *P. nebulifer* are more uniformly pigmented with less pronounced vertical barring than

TABLE 2
Body Proportions of Larvae and Early Juveniles of California *Paralabrax* species

Body proportion*	*Paralabrax clathratus*	*Paralabrax nebulifer*	*Paralabrax maculatofasciatus*
Snout to anus/body length			
Preflexion	529 ± 15 (500-553)	512 ± 12 (500-529)	520 ± 35 (484-556)
Flexion	564 ± 36 (527-613)	577 ± 21 (551-604)	553 ± 35 (521-621)
Postflexion	594 ± 16 (574-621)	582 ± 18 (565-608)	611 ± 18 (597-646)
Juvenile	606 ± 10 (589-628)	607 ± 10 (598-618)	626 ± 14 (607-650)
Head length/body length			
Preflexion	240 ± 27 (200-283)	255 ± 11 (235-270)	224 ± 8 (214-235)
Flexion	335 ± 24 (309-356)	336 ± 23 (306-368)	299 ± 28 (261-345)
Postflexion	375 ± 21 (360-408)	369 ± 18 (353-392)	354 ± 9 (342-364)
Juvenile	386 ± 18 (352-408)	376 ± 7 (369-385)	373 ± 17 (338-389)
Snout length/head length			
Preflexion	258 ± 20 (240-280)	248 ± 45 (150-308)	233 ± 26 (200-267)
Flexion	291 ± 16 (273-312)	264 ± 26 (222-286)	242 ± 24 (200-267)
Postflexion	265 ± 29 (222-306)	241 ± 22 (214-267)	250 ± 16 (226-273)
Juvenile	261 ± 32 (212-327)	221 ± 21 (200-244)	224 ± 32 (190-262)
Eye diameter/head length			
Preflexion	335 ± 46 (280-428)	295 ± 38 (250-356)	337 ± 16 (311-350)
Flexion	276 ± 32 (235-312)	295 ± 25 (267-333)	276 ± 20 (240-300)
Postflexion	273 ± 19 (250-306)	267 ± 18 (242-286)	282 ± 15 (273-303)
Juvenile	251 ± 20 (210-293)	280 ± 17 (255-293)	298 ± 21 (273-341)
Body depth at pectoral fin base/body length			
Preflexion	155 ± 18 (133-196)	184 ± 20 (159-223)	173 ± 25 (143-200)
Flexion	263 ± 45 (218-323)	260 ± 32 (204-265)	227 ± 36 (186-293)
Postflexion	289 ± 12 (265-310)	288 ± 15 (271-307)	288 ± 16 (273-314)
Juvenile	296 ± 13 (273-321)	297 ± 5 (294-304)	304 ± 12 (290-323)
Caudal peduncle depth/body depth			
Preflexion	—	—	—
Flexion	—	—	—
Postflexion	126 ± 13 (88-140)	129 ± 6 (122-136)	128 ± 15 (107-146)
Juvenile	130 ± 8 (122-143)	140 ± 5 (134-145)	153 ± 5 (148-162)
Caudal peduncle length/body length			
Preflexion	—	—	—
Flexion	—	—	—
Postflexion	166 ± 7 (159-176)	146 ± 14 (136-168)	160 ± 10 (146-177)
Juvenile	157 ± 6 (148-165)	149 ± 10 (134-156)	145 ± 7 (136-157)

*Values given for each body proportion expressed as thousandths of body length or head length: mean, standard deviation, and range.

P. clathratus. They have horizontal stripes that are less dense than those of *P. maculatofasciatus*. Large juveniles have a conspicuous diagonal pigment bar below the eye, and two short diagonal bars anterior to the pectoral fin base.

Description. Morphometrics of *P. nebulifer* are presented in Tables 2 and 3. Preflexion larvae are similar to the other two species, but differ in the sequence and detail of pigmentation. The posterior dorsal melanophore is lost at 3.4 mm, in contrast to its loss at 4.6 mm in *P. clathratus* (Figure 5A). The marginal pigment of the abdominal fin fold is comparatively heavier than in the other two species and usually appears as a continuous line. The postanal ventral midline pigment is a continuous series of uniform melanophores from the end of the gut to near the end of the notochord. Pigment appears in the horizontal septum above the anus (Figure 5B) by 3.6 mm.

During notochord flexion additional pigment appears along the horizontal septum above the gut, along the sides of the gut, and on the body below the dorsal fin (Figure 5C). Similar pigment appears in flexion larvae of *P. maculatofasciatus*. Although subtle differences in pigmentation exist between reared specimens of *P. nebulifer* and *P. maculatofasciatus*, identification of field-collected larvae undergoing notochord flexion may not be possible.

Postflexion larvae between 6 and 11 mm add pigment on the head, and on the snout and operculum to form a line of pigment across the eye (Figure 5E). Pigment also appears on the cranium and below the base of the spinous dorsal fin. Late-stage larvae lack the incipient body bars present as dorsal pigment saddles in *P. clathratus* and are generally lighter in pigmentation than late-stage *P. maculatofasciatus* larvae.

Metamorphosis occurs at about 11 mm. The juveniles become heavily and more uniformly pigmented than *P. clathratus* (Figure 6). A dark stripe extends from the snout through the eye and along the lateral line to the base of the caudal fin. A second stripe runs from the base of the pectoral fin to the caudal fin base. The stripes are interrupted by six faint

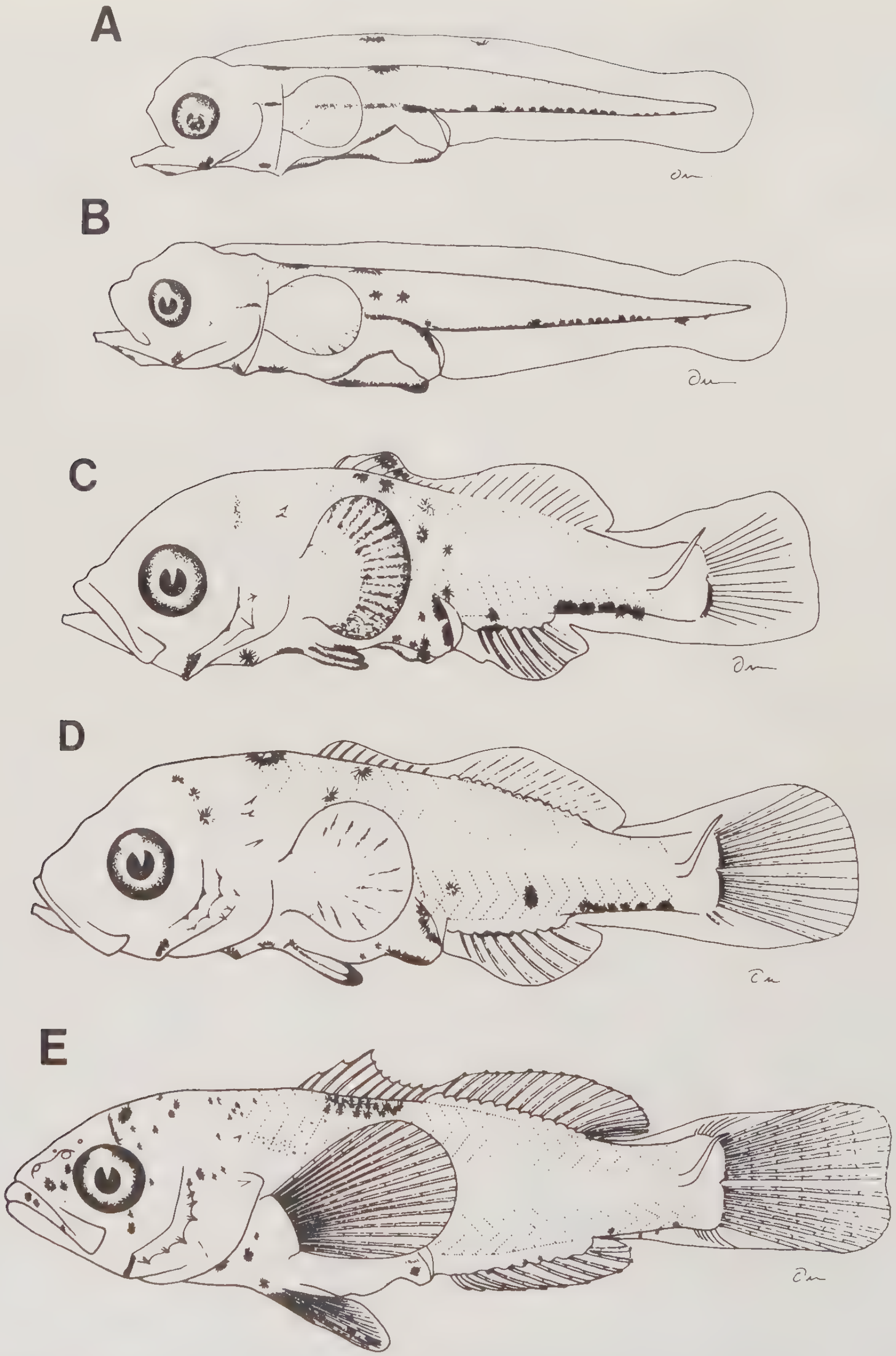

Figure 5. Larvae of *Paralabrax nebulifer*: *A*. 3.4-mm preflexion larva, 11 days; *B*. 4.4-mm preflexion larva, 10 days; *C*. 5.7-mm flexion larva, 29 days; *D*. 6.8-mm postflexion larva, 22 days; *E*. 9.4-mm postflexion larva.

TABLE 3
Measurements (mm) of Barred Sand Bass, *Paralabrax nebulifer*

Age (days)	Body length	Snout to anus	Head length	Snout length	Eye	Body depth at P_2	Caudal peduncle depth	Caudal peduncle length
11	3.4	1.8	0.8	0.12	0.28	0.76		
14	3.6	1.8	0.9	0.2	0.32	0.64		
11	3.6	1.8	0.9	0.2	0.28	0.64		
14	4.0	2.0	1.0	0.28	0.28	0.68		
14	4.2	2.1	1.1	0.28	0.28	0.72		
—	4.2	2.2	1.1	0.3	0.3	0.8		
10	4.4	2.3	1.1	0.3	0.3	0.72		
16	4.5	2.3	1.2	0.3	0.3	0.8		
17	4.8	2.5	1.3	0.4	0.4	1.0		
22	4.9	2.7	1.5	0.4	0.4	1.0		
25	5.5	3.1	1.8	0.4	0.6	1.5		
29	5.7	3.4	2.1	0.6	0.6	1.6		
22	6.8	4.1	2.3	0.6	0.7	1.8		
—	8.5	4.8	3.0	0.8	0.8	2.5	1.1	1.2
—	8.8	5.1	3.3	0.8	0.9	2.7	1.2	1.2
—	9.2	5.3	3.3	0.8	0.8	2.6	1.2	1.3
—	10.7	6.8	4.2	0.9	1.2	2.9	1.3	1.8
—	11.7	7.0	4.5	1.1	1.3	3.5	1.7	1.8
28	12.5	7.5	4.7	1.1	1.2	3.8	1.8	1.9
—	15.7	9.7	5.8	1.2	1.7	4.6	2.1	2.1
35	16.0	9.8	6.0	1.2	1.7	4.7	2.2	2.5

Specimens between dashed lines are undergoing notochord flexion.

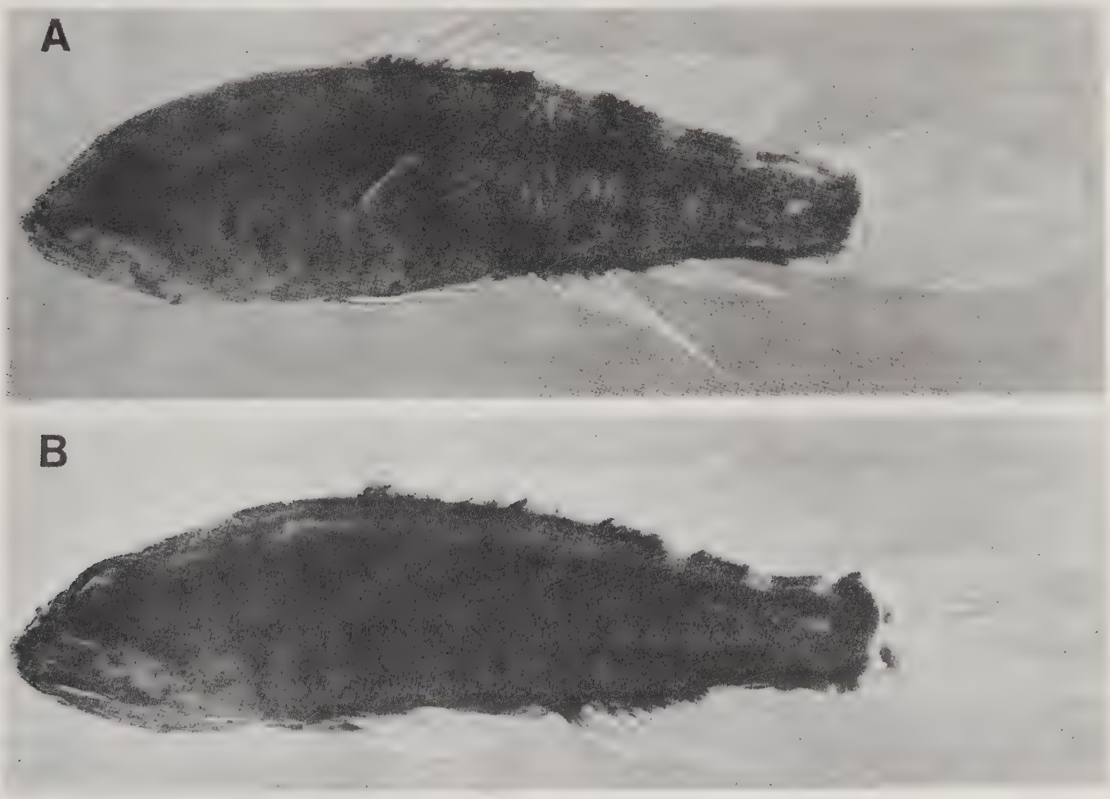

Figure 6. Juveniles of *Paralabrax nebulifer*: *A.* 10.8-mm newly transformed juvenile; *B.* 13.3-mm juvenile, 28 days.

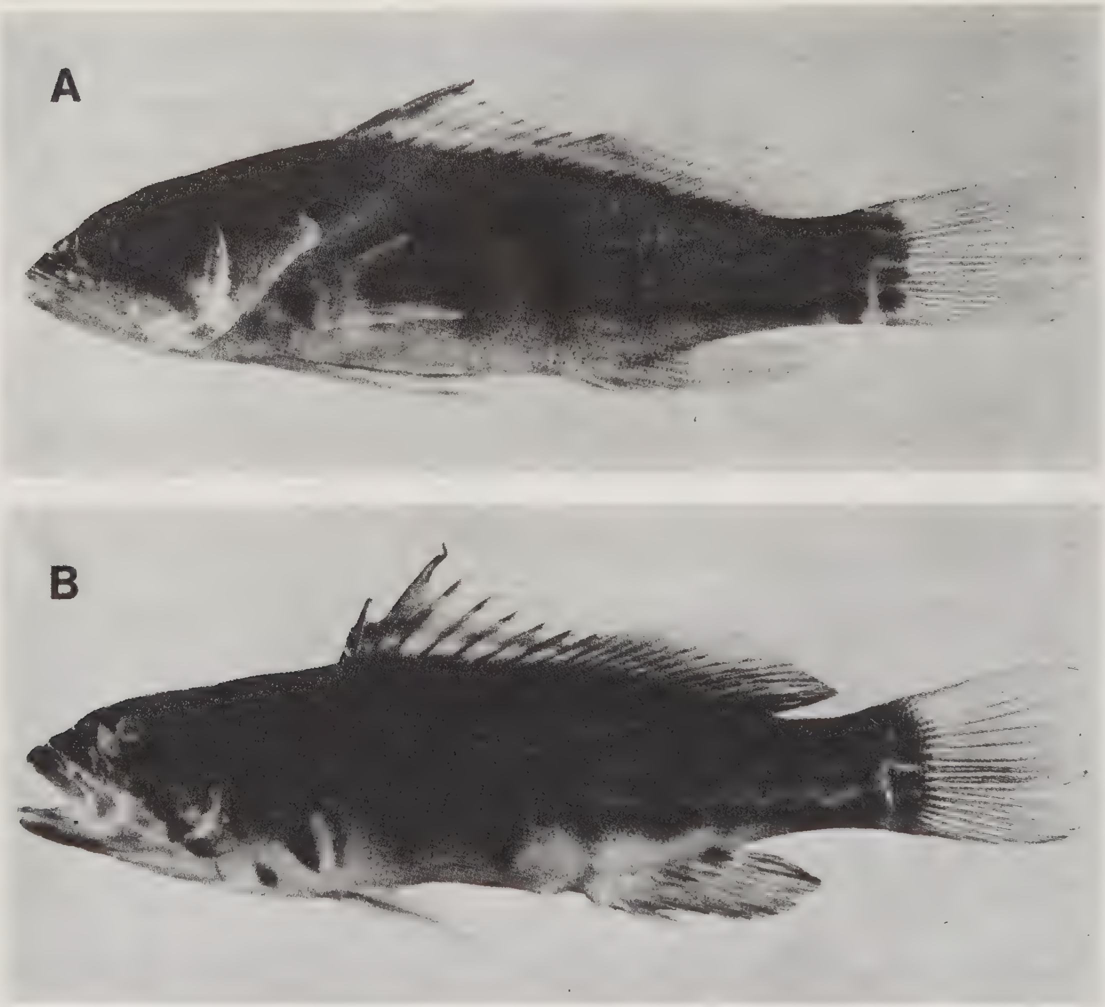

Figure 7. Juveniles of *Paralabrax nebulifer*: *A*. 33-mm juvenile, SIO 73-345, Mission Bay, San Diego; *B*. 45-mm juvenile, 99 days.

vertical bars: two beneath the spinous dorsal fin, two between the soft dorsal and anal fins, one on the caudal peduncle, and one over the hypural region. The bars extend onto the bases of the dorsal and anal fins (Figure 7). In larger juveniles the axial stripe and the upper portions of the bars blend with the uniformly heavy dorsal pigmentation; however, the bars are readily distinguishable ventrally (Figure 7). Juveniles at this stage have a prominent diagonal bar below the eye and two short diagonal bars anterior to the pectoral fin base (Figure 7).

Paralabrax maculatofasciatus ***(Steindachner 1868)*** ***Spotted Sand Bass*** **(Figures 8-10)**

Distinguishing characters. Preflexion larvae of *P. maculatofasciatus* may be distinguished from those of *P. clathratus* by the shape of the melanistic blotch on the preanal abdominal fin fold and by the absence of a third dorsal midline melanophore in larvae larger than 3.0 mm. Melanistic pigment is almost continuous along the ventral margin of the abdominal fin fold and does not form a triangular patch. Preflexion larvae of *P. maculatofasciatus* may be distinguished from those

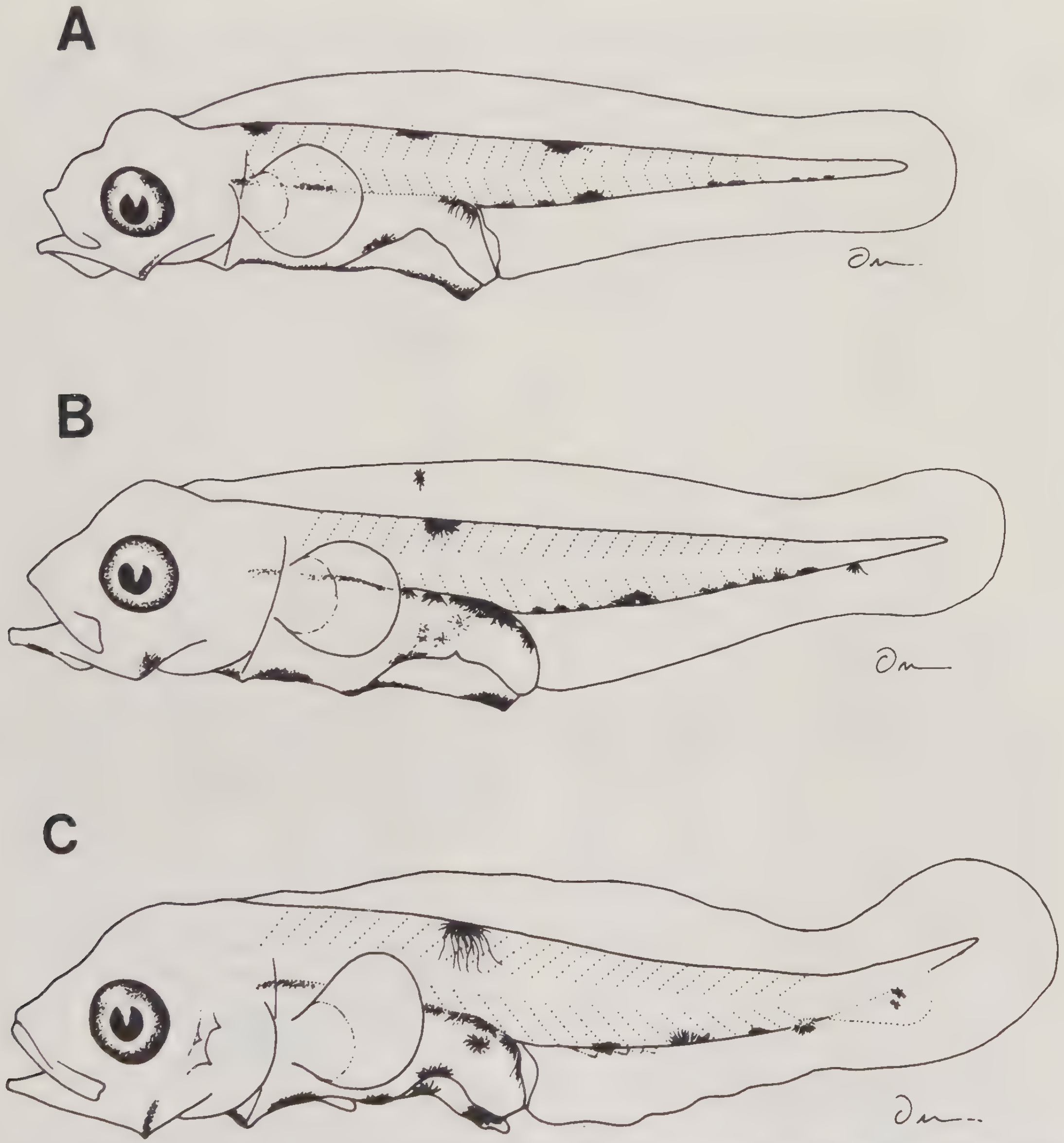

Figure 8. Larvae of *Paralabrax maculatofasciatus*: *A*. 3.1-mm preflexion larva, 5 days; *B*. 3.6-mm preflexion larva, 8 days; *C*. 4.5-mm preflexion larva, 12 days.

of *P. nebulifer* by the absence of horizontal septal melanophores and by their discontinuous and nonuniform ventral tail pigment.

Flexion larvae of *P. maculatofasciatus* can be distinguished from those of *P. clathratus* by the presence of melanophores along the horizontal septum and on the trunk. Flexion larvae of the two species of sand basses appear to be indistinguishable.

Late postflexion larvae of *P. maculatofasciatus* are distinguished from both *P. clathratus* and *P. nebulifer*

TABLE 4
Measurements (mm) of Spotted Sand Bass, *Paralabrax maculatofasciatus*

Age (days)	Body length	Snout to anus	Head length	Snout length	Eye	Body depth at P_2	Caudal peduncle depth	Caudal peduncle length
2	2.2							
4	2.8	1.4	0.6	0.16	0.20	0.40		
5	3.1	1.5	0.7	0.16	0.24	0.48		
8	3.4	1.9	0.8	0.16	0.28	0.68		
8	3.6	2.0	0.8	0.20	0.28	0.7		
9	4.0	2.0	0.9	0.20	0.28	0.7		
13	4.3	2.3	1.2	0.24	0.32	0.8		
12	4.5	2.4	1.3	0.32	0.36	0.9		
13	4.6	2.5	1.2	0.32	0.36	1.0		
14	4.8	2.5	1.4	0.32	0.4	1.0		
13	5.0	2.7	1.5	0.4	0.4	1.2		
23	5.2	3.0	1.7	0.4	0.5	1.3		
23	5.8	3.6	2.0	0.5	0.6	1.7		
19	6.2	3.7	2.2	0.6	0.6	1.7	0.7	1.1
26	7.5	4.6	2.7	0.7	0.7	2.1	0.8	1.2
21	7.7	4.6	2.8	0.7	0.8	2.1	1.0	1.2
23	8.2	5.0	2.8	0.7	0.8	2.4	1.1	1.3
23	8.6	5.2	3.1	0.7	0.9	2.7	1.2	1.4
25	9.6	6.2	3.3	0.8	1.0	2.8	1.4	1.4
33	10.3	6.7	4.0	0.8	1.2	3.1	1.6	1.4
33	10.8	6.7	4.2	1.1	1.2	3.2	1.6	1.7
28	11.8	7.5	4.4	0.9	1.2	3.6	1.8	1.7
35	13.0	8.2	4.4	1.2	1.5	4.2	2.1	1.9
40	14.5	9.0	5.5	1.2	1.6	4.2	2.2	2.0
38	16.8	10.2	6.3	1.2	1.9	5.0	2.5	2.5
35	18.0	11.2	6.7	1.5	2.0	5.7	2.7	2.6

Specimens between dashed lines are undergoing notochord flexion.

by the heavy pigment over the trunk. Juvenile *P. maculatofasciatus* develop a strongly contrasting stripe that extends from the snout through the eye to the caudal peduncle.

Description. Morphometrics of *P. maculatofasciatus* are given in Tables 2 and 4. Early preflexion larvae of *P. maculatofasciatus* are similar to those of *P. clathratus* in having three dorsal contour melanophores and several rather large melanophores along the ventral midline of the tail (Figure 8A). The line of pigment is almost continuous along the ventral margin of the abdominal fin fold. At about 3.6 mm, the posteriormost dorsal midline melanophore is lost. In some specimens the anteriormost dorsal melanophore is also lost (Figure 8B). After this, no significant pigment changes take place until notochord flexion.

During notochord flexion, lateral pigment is added over the gut, along the horizontal septum, and below the developing dorsal fin (Figure 9A). Following notochord flexion, pigment is augmented over the anterior portion of the trunk, and a conspicuous line of pigment develops on the head from the snout through the eye onto the operculum (Figure 9B and C). At about 11 mm, the conspicuous dark line extends from the snout to the caudal peduncle. A second horizontal stripe broken by unpigmented areas forms along the dorsum from the nape to the second dorsal fin during transformation (Figure 10A). At this stage, a third stripe begins to form from the base of the pectoral fin to the lower base of the caudal fin. The juvenile pigment is characterized by the three prominent stripes, with a background of six vertical bars similar in position to those on *P. nebulifer*. In larger juveniles the bars become larger and more conspicuous and begin to mask the stripes (Figure 10C). Pigment areas begin to break up into spots, a feature that characterizes the adults (Figure 10C). The cheek and lower opercular region are covered with large spots, and the pigment pattern forward of the pectoral fin consists of three distinct spots arranged in a triangle.

DISCUSSION

We have used laboratory-reared larvae as the basis for these descriptions. Pigment in laboratory-reared specimens is often more heavily expressed and certainly better preserved than in field-collected specimens. Considerable variability in pigmentation was observed in the laboratory series. Because of abrasion in the net and differences in preservation, field-collected specimens often lack important characters. In particular, fin folds are seldom present on net-collected larvae. Therefore, some field-collected

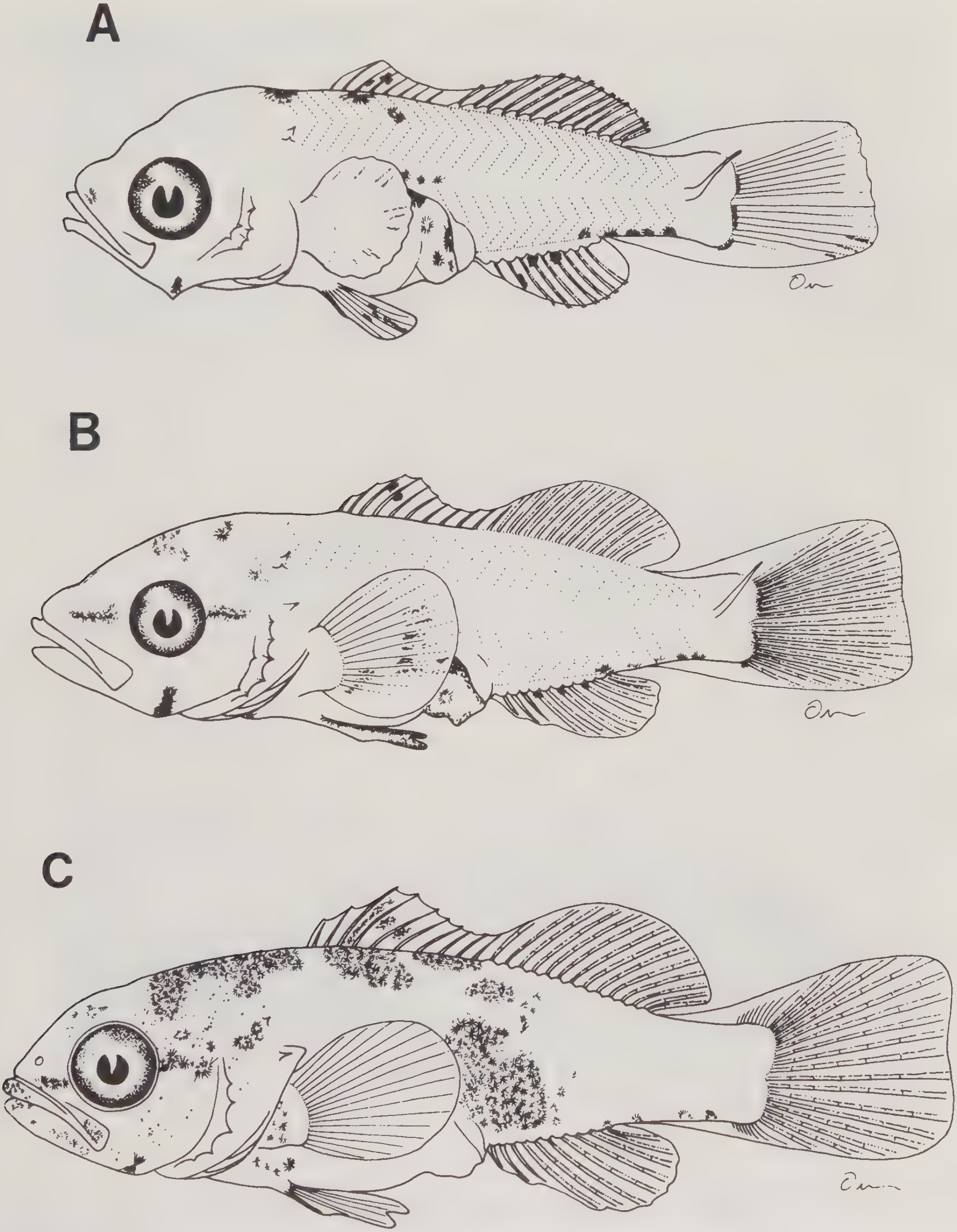

Figure 9. Larvae of *Paralabrax maculatofasciatus*: *A.* 5.8-mm flexion larva, 23 days; *B.* 7.9-mm postflexion larva, 26 days; *C.* 9.3-mm postflexion larva, 26 days.

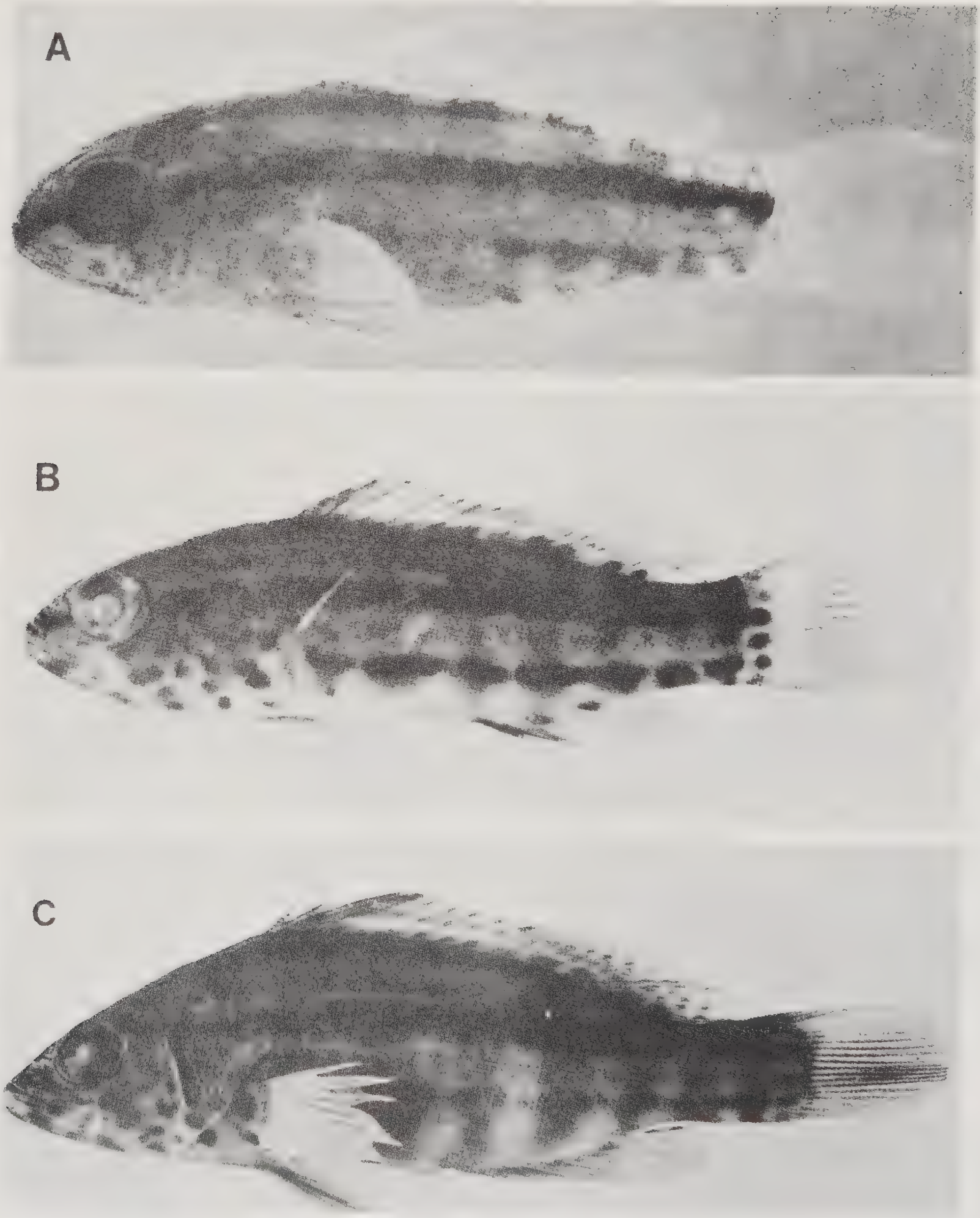

Figure 10. Juveniles of *Paralabrax maculatofasciatus: A.* 12.3-mm juvenile, 40 days; *B.* 29.5-mm juvenile, 49 days; *C.* 46-mm juvenile, SIO 73-345, Mission Bay, San Diego.

specimens often lack important characters. These descriptions are meant as an aid for identifying very similar larvae.

ACKNOWLEDGMENTS

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Predator-Prey Studies of the Shortbelly Rockfish

Offshore Sampling Problems

James R. Chess
National Marine Fisheries Service

Investigations of predator-prey relationships that have considered aspects of prey distribution and availability have, with few exceptions, been confined to well defined sites or areas where precise sampling and/or direct observations can be made. Most such studies have been conducted nearshore, where logistical problems are reduced and where direct observations are often feasible (e.g. Hobson 1968, 1974: Hobson and Chess 1976; Van Blaricom 1977; and Cailliet et al. 1979). Comparable investigations have dealt most often with organisms like flatfishes that live on the sea floor where methods for collecting benthic predators and prey species are relatively precise (e.g. Pearcy and Hancock 1978; Gabriel and Pearcy 1981). When offshore midwater sampling is required, problems arise which are not encountered in most nearshore or offshore benthic studies.

The variations in temporal and spatial distribution patterns of both predators and prey in this large three dimensional environment contribute to inconsistent sampling, especially of the predators. Furthermore, because of the dynamics of the water column and the patchy distribution of the plankton and planktivores, the interpretation of plankton samples that are intended to represent prey availability is often difficult, i.e. do the samples adequately reflect the actual prey items available to the predators.

Shortbelly Rockfish

The shortbelly rockfish, *Sebastes jordani*, is a large unfished resource in waters off California. During the past several years however, there has been a growing interest in the development of a fishery by fishermen and processors (Lenarz 1981).

A major portion of the shortbelly population occurs between latitude 36°56' and 37°21' (Gunderson and Sample 1980). In this area they appear to aggregate on the continental shelf and slope near submarine canyons or steep dropoffs at depths between 128 and 275 meters.

The shortbelly reaches maturity at about 16.5 cm and attains a maximum size of about 33 cm (Lenarz 1981), an appropriate-sized forage species for larger predators. This species is known to be an important item in the diet of king salmon off San Francisco (Merkel 1957).

Determining the value of shortbellies as a forage species for other large predators and understanding the dynamics of its own predatory activities is important before a large shortbelly fishery is established. It is unusual that the opportunity to study a commercially valuable species has arisen prior to its exploitation.

Objectives of the Study

Originally, the objectives in studying the trophic relationships of the shortbelly were to determine: a. its importance as a forage species, b. diel feeding patterns and prey selectivity, c. seasonal distribution and prey, d. depth/size relationships, and e. the variations in prey selectivity within various size classes.

All but the first, continue to be goals of the study. The collection of guts from the larger predatory fish from trawl samples proved unsatisfactory because of regurgitation of gut contents during trawl retrieval. So the role of shortbellies as a forage species is being considered in another segment of the overall program that samples these predators from sportfishing boats.

Study Areas

Beginning in the spring of 1979, when shiptime was offered by the Northwest Alaska Fisheries Center, attempts were made to locate specific sites where shortbellies aggregated. Our study of diel feeding patterns and prey availability is centered in an area of about 17 square kilometers on the shelf just west of Ascencion submarine canyon (37°00' N, 122°27' W). The bottom depths vary between about 120 and 200 meters. Our collections to determine size/depth distribution patterns and variations in prey selectivity with shortbelly size and depth are taken in an area less well defined near Pioneer Canyon (37°20' N, 23°00' W) where depths vary from about 120 to 275 meters.

Vessels

Twice during the first year of the study we used the NOAA ship Oregon. This vessel, however, was a trawler and not equipped to tow plankton nets. So no "prey samples" were obtained. It was well rigged and manned for trawling operations, though, and valuable data were gathered on distribution patterns of shortbellies. Also, during the first year we were able to use the NOAA ship Miller Freeman for 3 days. This ship had both trawling capabilities and elaborate acoustical fish monitoring equipment, in addition to standard oceanographic equipment. It enabled us to collect our first sample series of shortbellies and their prey. Since the fall of 1980 we have had the use of the NOAA ship David Starr Jordan on an approximate quarterly schedule. This ship, a well-equipped oceanographic vessel, had only limited trawling capabilities during the first three cruises. A recent refitting however, has dramatically increased its trawling capabilities, with improved net reel, door stanchions, hydroacoustic and navigational equipment.

Collecting Samples

We have determined from hydroacoustic tracings, that nearbottom daytime aggregations of shortbellies disperse up into the water column at night. To determine diel feeding patterns, gut samples are needed from both distribution modes, from periods immediately preceding daybreak and dark. Depth stratified plankton samples are also needed from midday and midnight periods to determine the diel distribution patterns of potential prey species.

A three-bridle midwater trawl with 100 ft headrope is used for collecting shortbellies for gut analysis and an opening/closing Tucker net with 1 m^2 effective opening is used for plankton collecting.

Sampling Problems

During this investigation the problems encountered center primarily around our inability to consistently collect adequate samples of shortbellies.

Locating shortbelly aggregations. To locate aggregations of shortbellies, hydroacoustic transects are made, usually in a zigzag or bathymetric pattern within the study area. Daytime shortbelly aggregations usually show a characteristic silhouette on sounder paper, being dense, round-topped and extending several to about 30 m from the bottom. Discrete nighttime aggregations are more difficult to identify. The shortbellies disperse into the water column, sometimes moving up as far as the lower portions of the near surface deepscattering layer, where they mix with other fish species that rise into the water column at night.

The acoustic resolution is variable with the different quality sounders on the various vessels, so the interpretation of target strength and shape and identifying them as shortbellies has often been a problem. A Simrad scientific sounder EK400 with high resolution has recently been installed aboard the Jordan and in the future should help us locate and identify fish aggregations. Scanning sonar helps considerably in locating fish aggregations but has been available to us only twice, once aboard the Miller Freeman and again aboard a chartered fishing vessel (Colintino Rose II).

Setting the trawl. If no acoustic targets are found prior to the sampling period, "blind" trawl sets are usually made at locations near where fish were previously found. As it has turned out, we have been just as successful in obtaining samples during these blind sets as when setting on acoustic targets. Reasons for missing targets have been one or a combination of the following: delays in setting due to deck gear problems, navigational limitations in returning to the target position, or fish movements and drift due to currents or wind.

With the recently installed plotter aboard the Jordan, our ability to return to specific targets has been greatly improved. The plotter is coupled with the Loran C navigational system and plots the track of the ship on paper, allowing return to any previously marked position.

The deck gear problems associated with trawl set delays have largely been solved by the recent installation of a split net reel, moving the net reel aft and constructing door stanchions.

Monitoring the trawl. Estimates of the trawl fishing depths were initially made by noting the presence or absence of benthic organisms. Adjustments to the trawl warp length were made in attempting to place the net just off the bottom. The warp length/depth ratios that developed were later modified by use of a time/depth recorder. But not until we were able to use a shipboard net monitoring system, with an acoustic link with the ship, were we able to observe the actual position of the trawl in relation to the bottom, surface and fish targets. This Furuno 200 net sonde has allowed us to more effectively fish the trawl and with a single exception (when about 25,000 lbs of shortbellies were collected during a 12 minute period), to monitor fish entering the trawl and thus limit trawling time in order to avoid unreasonably large samples. It also provides the opportunity to position the trawl, by varying warp length or ship speed to the depth of targets which are detected by the shipboard sounder.

Experience level of personnel. Another important factor contributing to our sample collecting limitations involves the lack of trawling experience of our biologists and technicians. Aboard the Oregon (a NOAA trawler) and the Colintino Rose II (a chartered fishing vessel) we usually had no problem catching shortbellies. Both of these ships were rigged and manned for fishing with experienced captains directing fishing operations. Aboard the Jordan, an oceanographic vessel, the cruise leader has that responsibility, and in our case, the cruise leaders have been relatively inexperienced, and have had difficulty in catching fish. Experience comes slowly when one fishes only 5 or 6 weeks per year. The problems considered in this report might seem naive to an experienced fisherman; however they have frustrated our field efforts significantly.

Conclusions

Most oceanographic vessels are poorly rigged for trawling operations. The specialized gear requirements for these operations are often incompatible with the ship design and refitting may be impractical as well as costly. The electronic equipment used in finding fish and monitoring trawls is costly and affording state-of-the-art instrumentation is out of the question for many scientific programs. However, to consistently collect fishes near bottom or in midwater with a trawl, a vessel that is properly designed and equipped for that purpose is required.

Perhaps equally important as the vessel and rigging is the presence of experienced personnel. In the shortbelly investigation, the presence of a qualified fisherman, hired to direct operations and to train the scientific participants early in the program, would surely have improved our successes and saved a great deal of valuable ship time.

The experiences gathered by all concerned with this shortbelly study as well as the recent modifications and equipment additions to the Jordan however, have improved our fishing successes.

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Distribution of Killer Whales in the Warm Temperate and Tropical Eastern Pacific

Marilyn E. Dahlheim[1], Stephen Leatherwood[2], and William F. Perrin[3]

ABSTRACT

Records of killer whale occurrence for the warm temperate and tropical eastern Pacific Ocean are summarized from 11 strandings/collections and 581 observations. Levels of sighting effort are identified and used to interpret trends in distribution and movement. Killer whales occur from the Gulf of California more or less continuously along the Pacific Coast from 35°N to just below 5°S. Nearly all records off California and western Baja California were within 150 nm of the coast. North of 20°N, there were only four widely scattered offshore sightings beyond 150 nm. South of 20°N, 56.6% of all sightings were within approximately 300 nm of the coast and 78.4% within 600 nm. Two offshore clusters of sightings occurred, (1) 7° to 14°N, 127° to 139°W and (2) within a band between the equator and 5°N from the Galapagos Islands to 115°W. Herds contained up to 75 animals, with a mean of 5.3 animals per herd. An estimated 91% of the herds contained fewer than 10 animals.

INTRODUCTION

Killer whales, *Orcinus orca,* are cosmopolitan in distribution. There are records of their occurrence from virtually all oceans and major seas and from all ocean zones (for review see Leatherwood and Dahlheim, 1978; Dahlheim, 1981). Concerning their relative abundance by habitat, Mitchell (1975) states that although reported from tropical waters and the open sea, killer whales appear to be most prevalent in the colder waters of both hemispheres, with centers of greatest abundance within 800 km of major continents. Details adequate to support summary statements about the species' distribution and relative abundance, however, have only been reported for four areas: northeast Atlantic (Jonsgård and Lyshoel, 1970); northwest Atlantic (Sergeant and Fisher, 1957); inland marine waters of Washington State, US and British Columbia, Canada in the northeast Pacific (Bigg, MacAskie and Ellis, 1976; Chandler, Goebel and Balcomb, 1977); and coastal Japan (Nishiwaki and Handa, 1958; Kasuya, 1971). Beyond the odd sighting record there is little or no published information currently available on such populations in other regions. This paper reviews the data available from 1907 through 1979 on killer whale occurrence in the eastern Pacific Ocean from latitude 15°S and longitude 160°W, north to latitude 35°N and east to the coastline (Fig. 1).

MATERIALS AND METHODS

Data collection and methods of analysis were the same as those used by Leatherwood, Perrin, Kirby, Hubbs and Dahlheim (1980) for Risso's dolphin, *Grampus griseus*. We reviewed all previously published and unpublished strandings and collections of killer whales in the study area. These data were summarized and their locations plotted and examined for distributional patterns (Fig. 2). All previously published data on sightings of killer whales were reviewed and tabulated.

We examined 306 unpublished observations of free-ranging killer whales from the National Marine Fisheries Service (NMFS) tuna-dolphin observer program (1974–79). An additional 275 unpublished at-sea sightings were available from our files and from the files of other individuals and agencies. We carefully examined these unpublished sighting records for reliability of identification. Interviews with observers and/or the use of photographs assured us of the accuracy of many records. Descriptions of animals with striking black and white coloration, a white oval eye patch, and prominent erect dorsal fin (all diagnostic field characteristics of *Orcinus orca*) aided in verification of the remainder. We discarded questionable records.

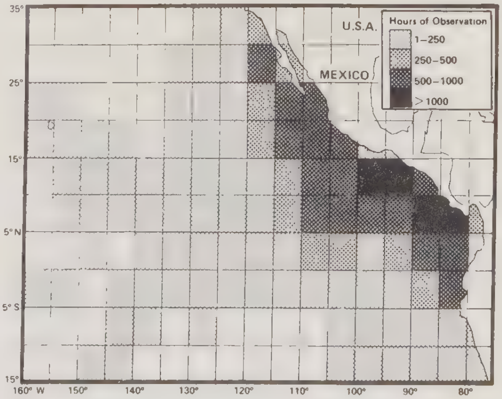

Fig. 1. Survey effort by NMFS dolphin-tuna observer program (1974–79), in hours of ship time by 5° square.

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[1] National Marine Fisheries Service, National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, 7600 Sand Point Way, N.E., Seattle, Washington 98115, USA; [2] Hubbs Sea World Research Institute, 1700 South Shores Road, San Diego, California 92109, USA; [3] National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038, USA.

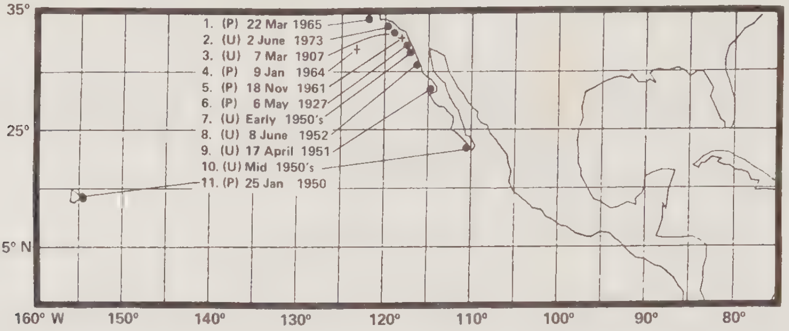

Fig. 2. Strandings (●) and collections (+) of killer whales (1907–79). (P) = Published record and (U) = Unpublished record. Numbers (1–11) refer to numbered paragraphs in the text.

Table 1

Principal sources of unpublished sighting records of killer whales in the study area. The two programs marked * maintained records of survey effort and are discussed in text

Institution/Activity	Approximate portion of study area covered	Approximate period and effort
I. US National Marine Fisheries Service		
A. Southwest Fisheries Center (Figs 1 and 3)		
1a. Dolphin-tuna observer program and associated research cruises	Principally lats 35°N to 15°S, coast to approximately long 160°N	1968–73—heavy effort nearshore Jan–Feb, declining and moving seaward throughout year, some coastward research Qtr. 4.
*1b. As above	As above	1974–79—generally as above, but effort data available as number of ship survey hours per 5° square (see Fig. 1).
B. National Marine Mammal Lab (Fig. 4)		
1. Research cruises	Lats 25°N to 35°N within 150 nm of shore[1]	1960s—sporadic coverage.
2. Pelagic Fur Seal Program	N of lat 32°N and E of long 130°W[1]	1960s—sporadic coverage.
II. Naval Ocean Systems Center (Fig. 3)		
A. Ship surveys	Within 100 nm of coast, So. Calif. & Baja Calif. and throughout Gulf of Calif.	1965–75—misc. cruises all seasons but principally winter and spring.
*B. Aerial surveys	Southern California Bight, above lat 32°N	1968–75—29,000 nm surveyed, representing all seasons (see Leatherwood and Walker, 1979).
III. Scripps Institution of Oceanography (Fig. 4)		
A. Research cruises	Principally within 100 nm of coast of California and Baja Calif, and in Gulf of California	1950–79—misc. cruises with no indication of survey effort by area or season.
IV. Smithsonian Institution Pacific Ocean Biological Survey (Fig. 4)	Lat 27°N to lat 35°N, coast to long 120°W	1967–68—unable to quantify effort by area or season.

[1] Principal program effort was farther north; effort in areas indicated was peripheral.

Additional sources include: The University of Southern California, the Natural History Museum of Los Angeles County, San Diego Museum of Natural History, Marineland of the Pacific, and numerous colleagues (Fig. 4).

Principal institutions contributing unpublished sighting records and statements of their effort in the area are listed in Table 1. Additional sources are referenced in acknowledgements. Records were grouped into two categories: (1) those sightings from the two programs in which effort has been quantified (NOSC aerial surveys, 1968–1975, and NMFS dolphin-tuna observer programs, 1974–79) and (2) miscellaneous sightings, including those for which there was no evidence of associated level of effort and those from programs for which effort could be only subjectively described.

For the NMFS dolphin-tuna observer program, 1974–79, effort—as number of ship survey hours per 5° square—and locations of sightings were plotted by quarter and examined for patterns of occurrence. All effort (Fig. 1) and sightings (Fig. 3) from all quarters were then combined and re-examined. For the years represented by this analysis, survey effort was sufficient at all seasons and latitudes for us to have detected major trends in distribution of cetacean fauna if they existed. Miscellaneous records were plotted (Fig. 4) and their distribution examined for evidence of patterns in killer whale occurrence.

Many of the sighting records included estimates of herd or group size. For those estimates stated as ranges (e.g. 10–20 animals), we used the midpoint for group size. If the midpoint was a half number, we rounded down.

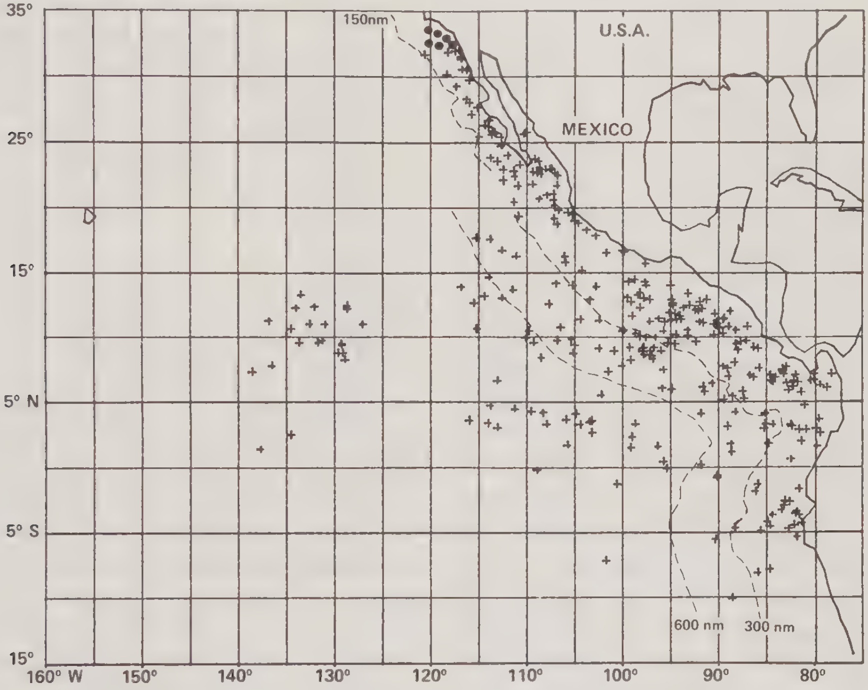
35°
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Fig. 3. Observations of killer whales by NOSC (●) and NMFS (+) programs (1968–79).

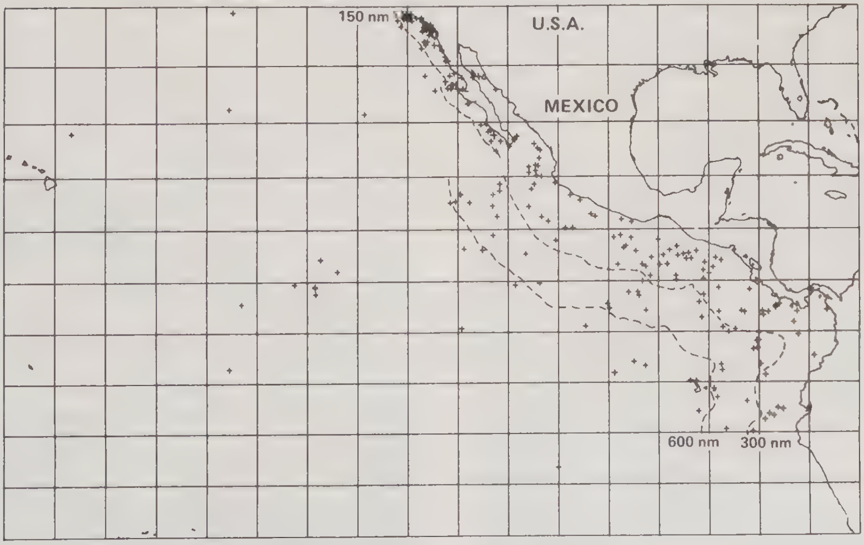
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Fig. 4. Miscellaneous observations of killer whales (1939–76).

RESULTS

Strandings and collections

We were able to find data for only 11 specimens of the killer whale in the study area: nine strandings, one live-capture, and one killed (Fig. 2). The letters in parentheses below indicate whether the record has (P) or has not (U) been previously published. Specimens are discussed below in chronological order:

3. (U) On 7 March 1907 the US National Museum, Smithsonian Institution catalogued a water-worn earbone (USM 49909) collected on an unspecified date by B. Traske at Avalon, Santa Catalina Island, California (James G. Mead, pers. comm., 16 June 1980).
6. (P) On 6 May 1927 a 'juvenile' killer whale of unreported sex and length was collected at Hermosa Beach, Los Angeles County, California (33°50′N, 118°25′W). The skull is in the collection of the Museum of Natural History of Los Angeles County—LACM 30461 (Caldwell and Brown, 1964).
11. (P) On 25 January 1950 an estimated 6.09 m (20 ft) male killer whale washed ashore on Ka Lae, South Point, Kau District, Island of Hawaii. No materials were collected and we have been unable to locate the photographs or additional data reportedly collected. This account constitutes the first published record of a killer whale from the Hawaiian Islands (Richards, 1952).
9. (U) On 17 April 1951 a partial skull was collected by W. Mayer at Viscaino Bay, Baja California, Mexico. This specimen is in the Los Angeles County Museum—LACM 22791 (John Heyning, pers. comm., 3 Oct. 1980).
8. (U) On 8 June 1952 Carl L. Hubbs uncovered a weathered skull of a killer whale at Punta Cabras, Baja California, Mexico, at approximately lat 31°20′N (Hubbs' field notes, 1952).
7. (U) On an unspecified date, thought to have been in the early 1950s (Laura Hubbs, pers. comm., 1978), a killer whale was found dead on the beach at Del Mar, California. We were unable to locate data or specimen material from the stranding.
10. (U) On an unspecified date, though to have been in the mid-1950s (Laura Hubbs, pers. comm., 1978), a killer whale was found dead on the beach at 23°25′N, 109°20′W. Apparently, no materials were collected.
5. (P) On 18 November 1961 a 5.21 m (17 ft) female killer whale was taken alive in a turning basin in the harbor of Newport, California (33°58′N, 117°55′W) and transported to Marineland of the Pacific, Palos Verdes, California, where it died two days later. Details of the capture, behavior, and postmortem examination of the whale are included in the account of the stranding (Caldwell and Brown, 1964). The complete skeleton of the specimen is in the Museum of Natural History of Los Angeles County (LACM No. 52455).
4. (P) On 9 January 1964 a free-swimming 5.65 m (18.54 ft) female killer whale was collected at 35°50′N, 120°31°W. The stomach contained remains of 2 moonfish and 2 carcharinid sharks. The skull is in the collection of the National Marine Mammal Laboratory—NMML No. 9860 (Rice, 1968).
1. (P) On 22 March 1965 a 7.4 m (24.28 ft) male killer whale was collected at 34°23′N, 121°16′W. The stomach contained baleen and blubber of a minke whale, *Balaenoptera acutorostrata*. The skull is in the collection of the National Marine Mammal Laboratory—NMML 1965–4 (Rice, 1968).
2. (U) On 2 June 1973 a 3.30 m (10.83 ft) immature male killer whale was found dead on the beach at Willow Cove, Santa Cruz Island, California. This animal was estimated to have been less than 1.5 years old. The stomach contained miscellaneous remains of a young California sea lion, *Zalophus californianus*. The entire skeleton was collected and taken to the Natural History Museum of Los Angeles County—LACM No. 54444 (Leatherwood field notes, 1973).

At-sea sightings

We observed 19 published articles containing records or summaries of observations of free-ranging killer whales in the study area (Table 2). In addition we assembled 581 reliable previously unpublished sighting records (a complete list is available from the senior author).

The distribution of the 581 sightings, from sources dating 1939–79, can be summarized as follows. The six records from NOSC aerial surveys, 1968–75, and the 306 from NMFS dolphin-tuna observer program, 1974–79, are shown in Fig. 3. No significant differences were apparent in distribution by quarter which could not readily be explained by variable effort. Therefore, all effort (Fig. 1) and all sightings (Fig. 3) from this program were displayed as cumulative summaries for all years and months combined. In this form, the distribution of the sightings is very similar to that from the 269 miscellaneous records (Fig. 4). Records from both sources extend from the Gulf of California more or less continuously along the Pacific Coast from 35°N to just below 5°S. Nearly all records off California and western Baja California were within 150 nm of the coast. Above 20°N, there are only four widely scattered pelagic records beyond 150 nm. Below 20°N, 56.6% (223 of 394) of all records were within approximately 300 nm of the coast and 78.4% (309 of 394) of the records were within 600 nm of the mainland coast.

Of particular interest, however, are the two clusters of sightings which occurred, one in the same general offshore area where miscellaneous sightings were concentrated (7° to 14°N, 127° to 139°W), and a second within a band between the equator and 5°N from the Galapagos Islands to 115°W. There was no seasonal pattern apparent in occurrence of animals in either of these zones which could not be readily related to variable effort.

Of the 581 unpublished sighting records, 508 provided usable estimates of herd sizes. Distributions of estimated herd sizes from the two data sets were compared. Because they were not significantly different (ANOVA; $P = 0.05$) the herd size data were pooled and grouped by 5° latitudinal belts and by seasons. Number of animals sighted within a herd ranged from 1 to 75, with a mean of 5.3 animals per herd. About 91% of the herds observed contained fewer than ten animals (Fig. 5). No differences could be demonstrated among herd sizes from different areas (5° bands of latitude) or among seasons (ANOVA; $P = 0.05$).

Table 2

Previously published at-sea observations of killer whales in the eastern North Pacific.

Source	Date	Location	Number in herd
Lacépède (1804)	Unreported	08°15′N, 79°00′W	Unreported
Scammon (1874)	Unreported	Off southern Calif. and the Baja Peninsula	Unreported
Banks (1931)	Unreported	24°45′N, 110°34′W	2
Allen (1939)	Unreported	32°51′N, 117°19′W	Unreported
Anonymous (1951)	9 May 1951	32°35′N, 117°15°W	Unreported
Brown & Norris (1956)	29 Oct 1954	34°10′N, 119°50′W	5
	3 Nov 1954	34°25′N, 119°40′W	7
	4 Nov 1954	33°45°N, 118°30′W	2
	18 Dec 1954	33°45′N, 118°30′W	11
	28 Dec 1954	33°45′N, 118°30′W	10
	14 Dec 1955	33°45′N, 118°30′W	1
	Unreported	25°00′N, 141°45′W	Unreported
Harder & Johannessen (1960)	Unreported	03°30′N, 141°45′W	Unreported
Van Gelder (1960)	Unreported	30°30′N, 116°06′W	4
Anonymous (1961)	28 Oct 1961	32°50′N, 117°19′W	10
Norris & Prescott (1961)	1940	Estero de Punta Banda, Baja California, Mexico	Unreported
	? May 1949	33°45′N, 118°30′W	3
	? Apr 1952	24°30′N, 111°45′W	5–7
	? Aug 1955	33°30′N, 119°00′W	6
	25 Nov 1956	33°36′N, 118°03′W	6
	1 Dec 1956	32°38′N, 117°17′W	8
	26 Nov 1958	Iron Bound Bay, Catalina Island	5
Lévèque (1963)	Unreported	Galapagos Islands	Unreported
Stephens (1963)	Unreported	Point Dume, Calif.	1
	? Mar 1959	28°20′N, 115°39′W	1
	? June 1960	La Jolla Cove, Calif.	4
	? Jan 1962	33°00′N, 117°10′W	1
	? Apr 1963	33°00′N, 117°00′W	4
Burrage (1964)	26 Jan 1964	32°50′N, 117°18′W	Unreported
Fiscus & Niggol (1965)	19 Mar 1958	34°05′N, 120°25′W	1
	6 Feb 1959	35°15′N, 121°54′W	2
	20 Feb 1959	34°39′N, 122°21′W	2
Leatherwood, Evans & Rice (1972)	Unreported	Notes distribution off So. California; Baja California, Mexico; and in pelagic tropical Pacific	Unreported
Gilmore (1976)	2 Sept 1953	La Jolla, California	3
	12 Apr 1954	La Jolla, California	16
	28 May 1954	La Jolla, California	4
	? July 1954	La Jolla, California	Unreported
	4 Sept 1954	La Jolla, California	3
	? Sept 1955	La Jolla, California	2
	25 Sept 1955	La Jolla, California	2
	20 Mar 1956	La Jolla, California	1
Norris et al. (1976)	Jan–Dec 1975–76	Southern California Bight	Unreported
Aguayo (1975)	Unreported	Notes distribution off Chile	Unreported
Leatherwood & Dahlheim (1978)	Unreported	Notes distribution California coast, around islands of Baja California, Mexico, and in the Gulf of California	Unreported

DISCUSSION

From the available data, strandings of killer whales in the study area would appear uncommon. The low frequency with which killer whales strand along the heavily populated and well-patrolled shores of southern California and extreme northwestern Baja California may be related to the apparent scarcity of killer whales in that area (see discussion of NOSC aerial surveys above; Norris, Dohl, Guero, Hobbs and Honig, 1976) or to a generally low tendency of this species to strand even when it is present in substantial numbers. For example, in the waters of Puget Sound, Washington, and British Columbia, where a population which numbers at least 216 individuals (and is seasonally supplemented by other emigrants) is carefully monitored (Bigg *et al.*, 1976) and well known to the public (Chandler *et al.*, 1977), only nine strandings have occurred in the last eight years (Michael Bigg, 20 May 1981, pers. comm.). Strandings of killer whales appear to be equally rare in other parts of the world.

Killer whales were seen frequently in near-shore parts of the study area south of southern California. However, few strandings were reported for that area. One cannot rule out the possibility that the low number of stranding records in most of the study area simply reflects the inaccessibility of much of the shoreline of Baja California, Mexico, Central America, and northwestern South America and the infrequency with which these shores are visited by scientists and others who take note of such events. Certainly, no seasonal or geographical patterns can be ascertained from the data currently available.

The overall concentration of records nearshore clearly reflects a concentration of effort in those areas by the fishery on which these data depended. In 1974–78, alone, most coastal zones were surveyed from 500 to over 1000 hours. Those coastal zones were fringed by a band of zones which were surveyed for 250 to 500 hours. Outside of those, westward and southward, there was little or no effort. Effort was heaviest in the early months of the year,

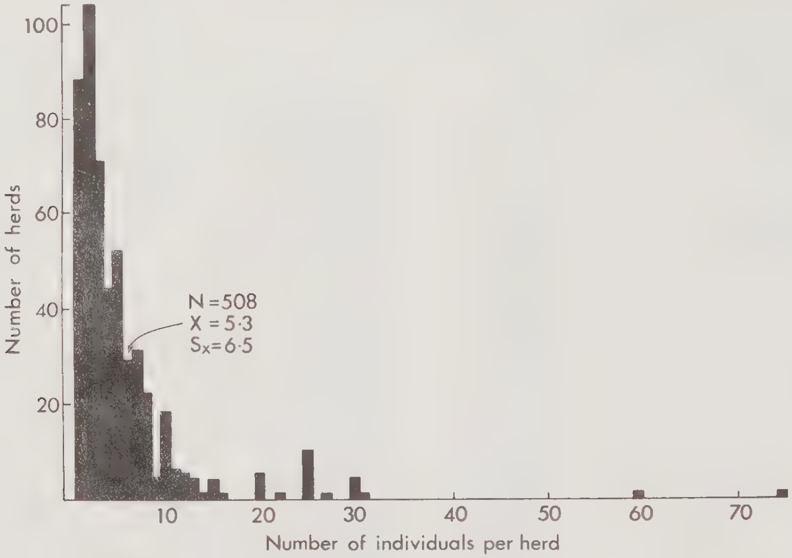

Fig. 5. Distribution of herd sizes of killer whales in the warm temperate and tropical eastern Pacific Ocean.

widely distributed but much of it concentrated near coasts. As the fishing season progressed that effort constricted in area and shifted its emphasis offshore and slightly southward (Au, Perryman and Perrin, 1979). The general decline in sightings offshore is, most likely, directly related to this pattern in effort. For that reason, the two areas of apparent offshore concentration are worthy of special note in that they occur within broad areas in which there were similar levels of effort but no sightings. Environmental features of the eastern tropical Pacific and their relationship to dolphin distribution are discussed by Au *et al.* (1979). These offshore concentrations of killer whales occur within the divergence zones of the North Equatorial Current and the Equatorial Counter Current, where other species of small delphinids have been reported. In the northwesternmost of these areas, similar concentrations are noted for bottlenose dolphins, *Tursiops* sp. (Walker, 1981) and pilot whales, *Globicephala* sp. (Reilly, 1977).

In other areas of the world, killer whale occurrence and movements have been related to movements of prey species, such as rorquals and seals off Canada (Sergeant and Fisher, 1957), herring off Norway and Iceland (Jonsgård and Lyshoel, 1970) and salmon in Puget Sound, Washington State (Balcomb, 1978). We do not know what killer whales feed on in the area covered by this report.

Herd sizes observed in the study area were smaller than those from the colder latitudes, where concentrations of 500 (Fiscus *et al.*, 1976) to 2,500 (J. Branson, Feb. 1980, pers. comm.) have been reported, but are consistent with those reported by Hall and Kelson (1959), 2–40 individuals, and Kasuya (1971), 1–30, $\bar{x} = 6$, for temperate waters.

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THE ESTIMATION OF SURVIVAL AND LITTER SIZE OF POLAR BEAR CUBS

DOUGLAS P. DEMASTER,[1] National Fish and Wildlife Laboratory, 108 Zoology Building, Minneapolis, MN 55455
IAN STIRLING, Canadian Wildlife Service, 5320–122nd Street, Edmonton, Alberta T6H 3S5

Abstract: The mark/recapture analyses that are currently used to study polar bears (*Ursus maritimus*) generally underestimate the average number of cubs per litter and assume that the annual survival of cubs is unity. In this paper, a relationship among the number of yearlings per litter and 2-year-olds per litter is used to derive the survivorship of yearlings, which is then used to solve for the number of cubs per litter. When this relationship was applied to published population data from North America, the resulting estimated survival rates of yearlings ranged from 0.70 to 0.75, and the estimated average number of cubs per litter was between 1.70 and 1.98. These findings indicate that current estimates of sustainable yield for polar bear populations may be in error because the reproductive rate of adult females was likely to be underestimated, and the survival rate of cubs of the year was likely to be overestimated.

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Obtaining estimates of a sustainable yield requires information on age-specific rates of reproduction and survival. For polar bears, the age-specific rate of reproduction equals the product of the average number of litters produced per year times the average number of cubs per litter for a female of age x. Satisfactory estimates of litter production rates are derived from mark/recapture information (Stirling et al. 1975; unpubl. rep., Environ. Manage. Serv., Edmonton, 1978; Lentfer et al. 1980). However, current estimates of the average number of cubs per litter are unreliable. For example, the estimate by Lentfer et al. (1980) of the average number of cubs per litter was less than their estimate of the average number of yearlings per litter. In addition, they found fewer litters of cubs than of yearlings. Obviously, there are sampling biases because the average number of cubs per litter cannot be less than the average number of yearlings per litter and there must be at least as many litters of cubs as of yearlings. However, in lieu of suitable alternatives, the average number of cubs per litter is assumed to equal the average number of yearlings per litter.

Inherent in the assumption that the number of cubs per litter equals the number of yearlings per litter is the assumption that mortality of cubs is zero. Unfortunately, survival rates for cubs have not been estimated. Standard age class estimates of survival of cubs are not possible because, in most studies, a greater number of yearlings are captured than cubs, and sample sizes are typically too small for mark/recapture studies to be of use. An additional problem with assuming that mortality of cubs is zero is that the average number of yearlings per litter is consistently greater than the average number of 2-year-olds per litter (Stirling et al. 1975; unpubl. rep., Environ. Manage. serv., Edmonton, 1978; Lentfer, unpubl. rep., Alaska Fed. Aid Proj. W-17-4/5, 1976; Lentfer, et al. 1980). This implies that yearling mortality is greater than zero; therefore, it is unlikely that the mortality rate of cubs is zero. The purpose of this paper is to present a method that estimates yearling survival from the difference between the number of yearlings per litter and the number of 2-year-olds per litter, and then to show how to use this rate to estimate the number of cubs per litter.

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THE MODEL

The basis for estimating yearling survival is the relationship between the mean litter size of animals age i and age $i+1$. Estimates are derived by assuming that the survivorship of a cub is independent of litter size; i.e., cubs from litters of

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[1] Present address: National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.

2 survive at the same rate as cubs from litters of 1. It is also necessary to assume that the survivorship of cubs is constant from year to year, and that litter sizes of 3 do not occur. Under these conditions, the expected litter size after 1 year is derived by a binomial process, except that litter sizes of zero are not observed.

For an initial litter size of 2 where s is the true annual survivorship of cubs, the probabilities, P, are:

$$P_2\ (\textit{2 cubs survive 1 year}) = s^2$$

$$P_1\ (\textit{1 cub survives 1 year}) = 2s(1-s)$$

$$P_0\ (\textit{neither cub survives 1 year}) = (1-s)^2.$$

For a litter size of 1, the probability of 1 cub surviving is s.

The relationship between survival and the litter size of young of age i and $i+1$ is derived as follows:

$$N_{i+1} = 2n_i s^2 p_i + 2n_i s(1-s)p_i + n(1-p_i)s$$
$$= n_i s(1-p_i),$$

where

N_{i+1} = the number of cubs of age $i+1$,

n_i = the number of litters of age i, and

p_i = the proportion of litters with 2 cubs of age i.

The numbers of litters of age $i + 1$ is then:

$$n_{i+1} = n_i s^2 p_i + 2n_i s(1-s)p_i + n_i(1-p_i)s$$
$$= n_i s(p_i - sp_i + 1).$$

Therefore, if $E(X_i)$ is the estimated average litter size in year i, the expected value of the litter size after 1 year, given the initial proportion of litters with 1 and 2 members, and given an annual survivorship of s, is:

$$E(X_{i+1}) = \frac{n_i s(1+p_i)}{n_i s(p_i - sp_i + 1)}$$
$$= \frac{(1+p_i)}{(p_i - sp_i + 1)} \qquad (1)$$

Because in any given year i,

$$E(X_i) = 2p_i + (1-p_i),$$

it can be easily shown that

$$p_i = \hat{X}_i - 1. \qquad (2)$$

When Eq. (2) is incorporated into Eq. (1), the result is:

$$E(X_{i+1}) = (\hat{X}_i - s\hat{X}_i + s). \qquad (3)$$

When estimates for X_i and X_{i+1} are available, Eq. (3) can be rewritten such that s is estimated by:

$$E(s) = \frac{(X_i - X_i X_{i+1})}{(X_{i+1} - X_i X_{i+1})} \qquad (4)$$

In addition, if it is assumed that the survivorship of cubs equals the survivorship of yearlings, Eq. (4) can be rearranged to estimate the average litter size of cubs:

$$E(X_i) = \frac{sX_{i+1}}{(1 + sX_{i+1} - X_{i+1})} \qquad (5)$$

APPLICATION OF THE MODEL

The survival rate of yearling polar bears, when estimated from the available data on the average number of yearlings per litter and 2-year-olds per litter, is relatively consistent between 4 different populations of polar bear (Table 1). These data indicate that yearling survival, given that the sow survives, is between 0.80 and 0.85. If adult survival equals 0.88 (Stirling et al., unpubl. rep., Environ. Manage. Serv., Edmonton, 1978; DeMaster et al. 1980), the estimated annual survivorship of yearlings is between 0.70 and 0.75. Estimates of yearling survival based on the ratio of successive age classes (number of yearlings/number of 2-year-olds) vary between 0.19 and 0.91 (Table 1). The wide range in survival estimates, based on the ratio of consecutive age classes, is primarily due to small sample sizes.

If it is assumed that the survival rate of cubs equals the survival rate of yearlings, Eq. (5) gives an estimated litter size for cubs of between 1.70 and 1.98. Considering that published estimates of the average number of cubs per litter ranged from 1.53 to 1.66 for this data set, it is clear that the proposed estimation procedure significantly departs from the previous approach.

The first assumption that the survival of cubs from litters of 1 equals the survival of cubs from litters of 2, is supported by data from 10 years of mark/recapture information on polar bears in Alaska, showing the proportion of cubs originally observed that were subsequently resighted as adults. Such resighting totaled 14 (20.0%) for 70 single-cub litters originally observed, and 31

Table 1. Observed litter sizes, from population studies of North American polar bears, and derived estimates of survival (from Eq. (4)) and original 1st-year litter size (from Eq. (5)). Yearling survival (y) is also estimated from the ratio of the number of yearlings to the number of 2-year-olds.

	Cubs			Yearlings			2-year-olds			Survival, *s*			Original litter size, E(*X*)
Data source	No. of litters	No. of cubs	Average litter size	No. of litters	No. of cubs	Average litter size	No. of litters	No. of cubs	Average litter size	Cubs	Yearlings	y	
Lentfer et al. (1980)	38	60	1.58	77	128	1.66	57	84	1.47	1.08	0.80	0.66	1.98
Stirling et al. (1975)	19	32	1.68	23	38	1.65	18	27	1.50	0.97	0.85	0.71	1.87
Stirling et al. (1980)	34	62	1.82	7	11	1.57	7	10	1.43	0.81	0.83	0.91	1.78
Stirling et al. (pers. comm.)	63	101	1.60	59	90	1.53	12	17	1.41	0.92	0.84	0.19	1.70

(15.2%) for 204 2-cub litters. These resighting rates are not significantly different ($X^2 = 0.88$, d.f. = 1). It is necessary to also assume that the survival of cubs is constant from year to year. There is no information to verify this assumption, but Stirling (unpubl. rep., Can. Wildl. Serv., 1978) reported that even in an unusually severe winter, the mortality of cubs was not significantly different from the mortality observed in more typical winters.

Finally, it is necessary to assume that litter sizes of 3 do not occur. Stirling et al. (unpubl. rep., Environ. Manage. Serv., Edmonton, 1978) and Lentfer et al. (1980) report litters of 3, but these are rare enough that in most areas of the Arctic their exclusion is not significant. Adoption is a potential mechanism that would also produce litters of 3. There is no evidence for adoption in any of the mark/recapture data from Alaska or Canada, and therefore we do not consider this a significant problem.

Predictions of the model seem reasonable where data exist to examine them. The consistent decrease in the number of yearlings per litter compared to the number of 2-year-olds per litter in the published literature indicates that mortality of yearlings is significant (Stirling et al. 1975, 1977; unpubl. rep., Environ. Manage. Serv., Edmonton, 1978; Lentfer, unpubl. rep., Alaska Fed. Aid Proj. W-17-4/5, 1978; Lentfer et al. 1980). It is not possible to estimate survival of cubs from existing data, but it has been speculated for other species of marine mammals that the survival of young of the year could be lower than that of any other age classes (Eberhardt 1977). It is therefore reasonable to expect cub survival to be less than unity.

There are 2 hypotheses that explain why published estimates for the mean number of cubs per litter are consistently low. The first states that litters of 1 may tend to be more mobile than litters of 2, and may therefore travel into ice types that investigators tend to search because of the increased visibility of polar bears. This would imply that the average distance between successive resightings of cub litters of 2 would be less than distances between successive resightings of cub litters of 1. A second hypothesis is that litters of cubs that are out in areas sampled by investigators experience higher mortality due to cannibalism by adult males than litters of cubs from areas less intensively studied. This implies that a near-shore sample of cub litters would have a higher mean litter size than an off-shore sample of cub litters. There are currently not enough data to test this hypothesis, but cannibalism of cubs by adult males has been reported (Stirling et al. 1975).

Additional data indicate that litter size estimates of 1.65 for cubs may be an underestimate. Data from zoos suggest that normally 2 young are born (Uspensky 1965; Harington 1968; Nunley 1977). In addition, polar bear populations in the Hudson Bay area typically have a mean number of cubs per litter between 1.8 and 2.0. However, this estimate of litter size may not be comparable with estimates of the number of cubs per litter from other areas because litters are larger in this area (Stirling et al. 1977) and litter size is determined from counts after families have left their dens but before they reach the sea ice.

Currently, estimates of the number of cubs per litter are generally assumed to equal estimates of the number of yearlings per litter. In addition, cub mortality is assumed to be insignificant. Because the average number of cubs per litter and the survival rate of cubs are important, statistics in the harvest models used to estimate sustainable yields, we recommend that the assumption concerning these statistics be reexamined. Small biases in either litter size or cub survival could result in serious errors in estimates of sustainable yields. For example, given a reproductive interval of 3.12 years (Lentfer, unpubl. rep., Alaska Fed. Aid Proj. W-17-4/5, 1976), a sex ratio of 1:1, and a mean cub litter size of 1.88, the annual rate of reproduction is approximately 0.30. However, if the mean cub litter size were 1.65, the rate of reproduction would be 0.26. The difference between 0.26 and 0.30 is critical for predicting sustainable harvests. Likewise, differences of roughly 0.15 in cub mortality are critical to the predictions of population models for polar bears. Given the current techniques in use, we feel that mortality of yearling polar bears is significant and that current estimates of the number of cubs per litter are negatively biased. We recommend that management practices be reviewed with these points in mind.

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Radio Telemetry of Hawaiian Green Turtles at Their Breeding Colony

ANDREW E. DIZON and GEORGE H. BALAZS

Andrew E. Dizon was with the Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812 and George H. Balazs is on an Intergovernmental Personnel Assignment from the Hawaii Institute of Marine Biology, University of Hawaii, to the NMFS Honolulu Laboratory. Dizon is now with the Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

ABSTRACT—Little is known about the range and movements of green turtles, Chelonia mydas, *during the critical period of their life history when they gather on their breeding grounds to copulate and nest. In order to investigate these behaviors, we developed radio telemetry techniques to determine position and environmental temperature. Access to the turtles is facilitated because Hawaiian* Chelonia *have a unique behavior of land basking. For about 3 weeks in the middle of the breeding season, we plotted the movements of four males and four females.*

This report concentrates primarily on tracking methods, but we also discuss the distribution of the turtles and their fidelity to the nesting beach. Although there are two nesting complexes of the breeding atoll and they are separated by 9 km, no movements between the two areas were observed. Both males and females remained in proximity to what we believe is their natal beach.

Introduction

More than 90 percent of the breeding activity of the Hawaiian green turtle, *Chelonia mydas*, occurs at a small atoll situated about midway along the 2,450 km length of the Hawaiian Archipelago (Fig. 1). Here, principally during May and June, turtles gather to copulate and nest.

Because of the specificity of the marine turtle's choice of breeding sites and times, any significant disturbance by man during this period could have profound effects upon the population. Yet little is known about the marine habitat of the animals during this period. Most of the work (Balazs, 1976, 1980) has involved hauled-out turtles when

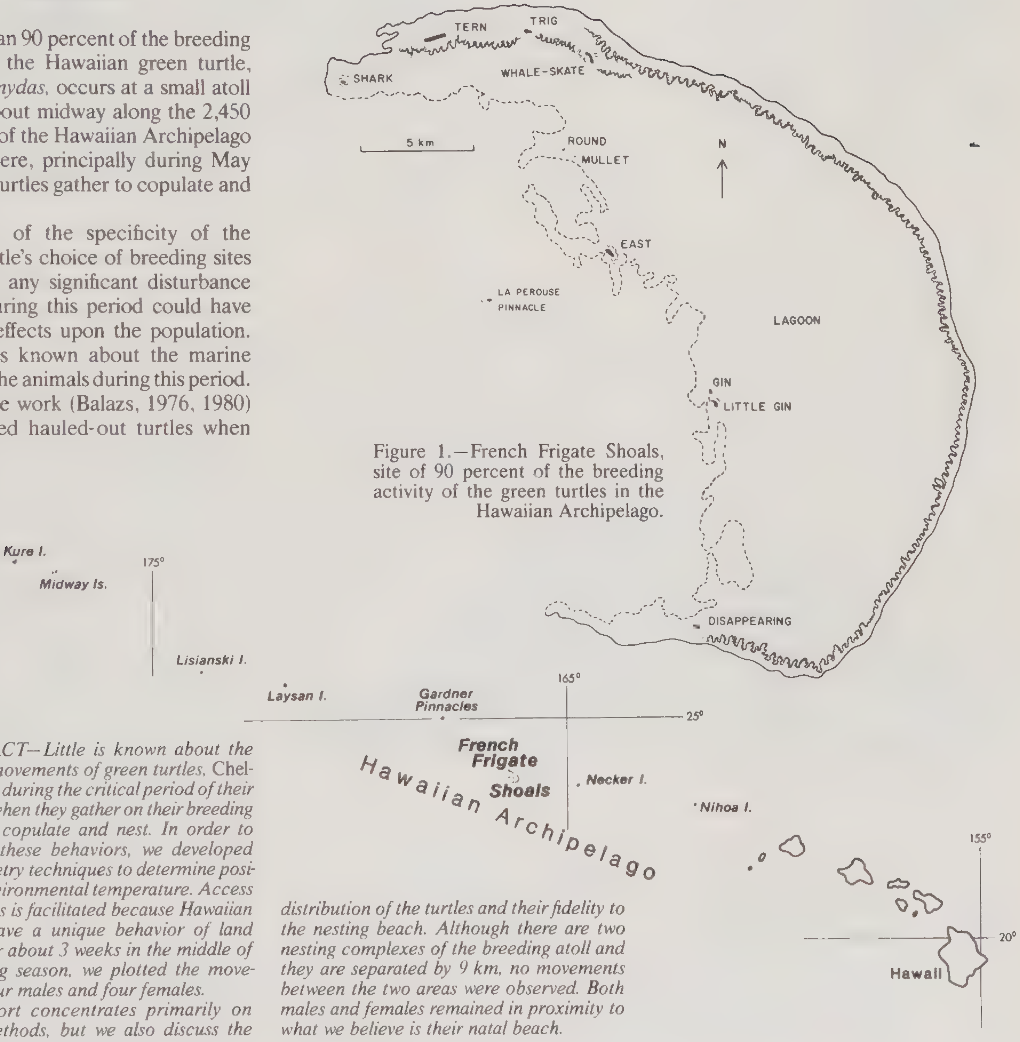

TERN
TRIG
SHARK
WHALE-SKATE
5 km
ROUND
MULLET
N
EAST
LA PEROUSE PINNACLE
LAGOON
GIN
LITTLE GIN
DISAPPEARING
Kure I.
175°
Midway Is.
Lisianski I.
Laysan I.
Gardner Pinnacles
165°
25°
French Frigate Shoals
Necker I.
Nihoa I.
Hawaiian Archipelago
155°
20°
Hawaii

Figure 1.—French Frigate Shoals, site of 90 percent of the breeding activity of the green turtles in the Hawaiian Archipelago.

they are readily visible to the investigator. Where the turtles go between the periods when they crawl out on the beach remains a mystery. Yet it is when the turtles are in the nearshore waters that the greatest potential for conflicts with humans exists. Managers of the habitat must be informed about the distribution of the turtles during the breeding period in order to avoid potentially damaging interactions.

The purpose of our study was to develop radio telemetry techniques to locate turtles throughout their breeding habitat and to study their range and behaviors during the breeding period. This report will concentrate primarily on the tracking technique and briefly describe the breeding habitat range. Specific details of their behaviors will be the subject of a subsequent paper.

Green turtle at French Frigate Shoals.

The Site

The breeding atoll is called French Frigate Shoals (FFS). It is a crescent-shaped platform which rises to within about 40 m of the surface (Amerson, 1971). Extensive reef growth has occurred on the platform and now there are about 12 permanent islands, 4 with well-established vegetation.

Tern Island, the largest, was modified during World War II to serve as a refueling base for aircraft support of the Midway Campaign. It was later used by the U.S. Coast Guard which maintained a loran station there until 1979. The U.S. Fish and Wildlife Service now maintains the island with several resident biologists. French Frigate Shoals as well as most of the other islands of the northwestern segment of the archipelago are units of the Hawaiian Islands National Wildlife Refuge and are designated officially as a Research Natural Area. Tern Island was the base of our operation.

The Turtles

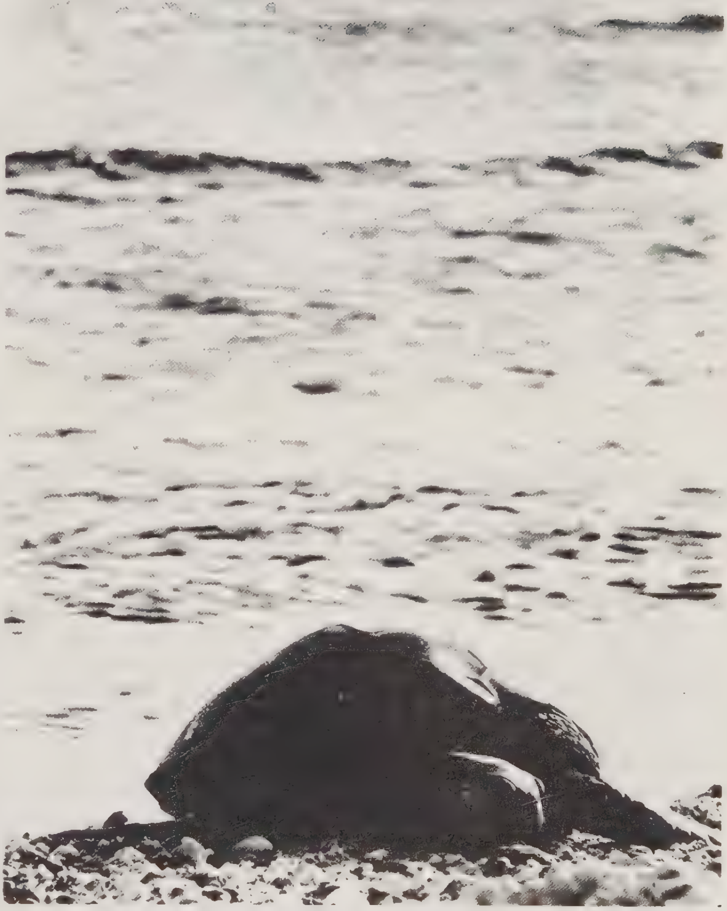
Work over the past 8 years on the turtles of FFS has revealed much about their natural history. The turtles arrive at the breeding atoll during mid-April to early June. Courtship and copulation take place then. Nesting starts as early as mid-May, peaking in June, and has all but ceased by mid-August. Nesting takes place over most of the larger stable islands with approximately 55 percent nesting at East Island and 35 percent at Whale-Skate/Trig Island complex (Fig. 1). As many as six egg clutches may be laid by a single female during one season but the mean is 1.8. The interval between oviposition in turtles that nest more than once averages 13 days, ranging from 11 to 18 days. Females journey to the breeding atoll once every 2 or more years; males every 1 or more years. The turtles come from and return to feeding pastures located in the rest of the archipelago. These long-range precise migrations to and from the breeding islands have been documented by the marking and subsequent recapture of 52 turtles (Balazs, 1976, 1980).

Hawaiian *Chelonia* exhibit a unique behavior which make them quite amenable to biological study. The turtles bask on land for extended periods both day and night, and while basking they are relatively easy to capture and tag. French Frigate Shoals is one of eight breeding colonies designated for high priority by the World Conference on Sea Turtle Conservation (1979) by reason of unique ecology and isolation. Balazs (1980) in a study period extending over 8 years has tagged over 140 adult male and 528 adult female turtles. Yet mark-and-recapture studies are not well suited for delimiting the critical habitat of the turtles during their sojourns within the nearshore waters between nesting or basking period on land. Extensive trapping in the water to recapture the marked animals is impractical. Identification marks painted on the shells allow for visualization of limited movements, but most turtles are quickly lost to the observer when they are not basking or nesting.

We felt that radio telemetry to determine movements was the least intrusive method of determining positions during trips away from the beach. We attached small transmitters to the turtle's carapace and fixed their positions by triangulation from two distant receiving stations. With this technique we were able to determine positions of the turtles during basking or swimming on the surface. As a result we were also able to ascertain the fraction of time the animals spent on the surface or on land and how much time submerged. These data are necessary to correct past and future census information since, at any one time, only a fraction of the turtles are visible to an observer. Our transmitters were sensitive to the environmental temperature so that we could determine whether turtles were basking on land or swimming at the surface. This information as well as other performance parameters of the turtles will be the subject of a subsequent paper. For now, we are interested in the techniques and range.

Past Telemetry Work Within Breeding Colonies

"One of the conspicuous gaps in the behavioral ecology of the green turtle . . . is the lack of data on the movements of females during the 12-14 day periods between their emergences at the nesting beach" (Carr et al., 1974). Actually, a number of studies have been conducted but more data still need to be generated (Carr, 1967a, 1967b, 1972; Baldwin, 1972; Meylan, 1978, in press; Standora et al., 1979; Feazel, 1980; Mortimer, 1981). The internesting movements of two other species have also been investigated (loggerheads, *Caretta caretta*, Murphy, 1979; Stoneburner, 1979; and Kemp's ridley, *Lepidochelys kempi*, Pritchard, 1980). All of these data are characterized by few subjects, no males, and short tracking periods. Most utilized a towed drogue usually equipped with a pennant and light. Sometimes sophisticated satellite transmitters were employed (Stoneburner, 1979; Daniel, 1980). Thus technical equipment is not cause for the information gap. Nor is size a problem since in fact telemetry devices (both radio and acoustic) are available for use on juveniles and hatchlings (Ireland, 1979a, 1979b; Garmon, 1981; Timko and DeBlanc, 1981; Stinson and Fritts[1]). Our goal was to deploy radio transmitters on both male and female turtles, track them throughout a significant portion of the reproductive period, and collect as many distributional, behavioral, and physiological data as possible.



Green turtle basking at French Frigate Shoals.

The Transmitters and Their Deployment on the Turtle

The 2 m (149 mHz) transmitters we employed were purchased as "off-the-shelf" items from Telonics, Inc.[2] Mesa, Ariz., (Fig. 2). These were hermetically encapsulated 7.5 × 4 × 3 cm, round-edged boxes with a mounting flange

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[1] M.L. Stinson, 1553 Avocado Drive, Vista, CA 92083; T. Fritts, National Fish and Wildlife Laboratory, Tulane University, Belle Chasse, LA 70037, pers. commun.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

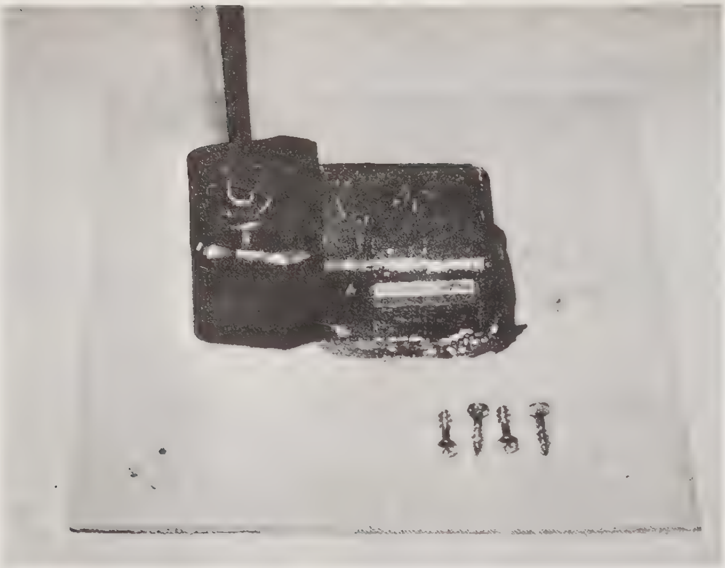

Figure 2.—The transmitter and its mounting plate. Note the thread design on the bone screws and the magnet which is used to turn the transmitter off.

attached to the bottom. A flexible quarter-wavelength stub antenna emerged from the front and extended 46 cm. The transmitters were temperature-sensitive; as the package warmed, the pulse rate increased. We observed an effective range of over 10 km when the transmitter package was awash at the sea surface and the receiving antenna was elevated about 9 m.

Since we were interested in following the animals for a long period, a reliable attachment method for the transmitter was critical to the success of the project. Hawaiian *Chelonia* have a habit of resting within coral caves and under outcroppings. A tethered transmitter would be useless and unless provided with a breakaway link, would pose a danger to the animals.

The study areas of the other workers reported earlier were generally free from such obstructions. Thus we had to attach the transmitter directly to the shell. To conform to the curvature of the shell and yet provide a wide mounting base, the transmitter was secured to a 15 × 15 cm, 0.6 cm thick piece of high molecular weight polyethylene (Fig. 2). This very tough but flexible plastic easily conformed to the carapace.

The plastic was attached to the shell with surgical bone screws fabricated for orthopedic repairs (mallolar style, Zimmer Inc.). The screws were made of a proprietary alloy which made them unreactive within the tissues of the shell and impervious to the seawater. The thread of the screw was designed to provide great holding power with the very shallow penetration which we required. Experiments with captive turtles demonstrated that the attachment technique was sound but the silvery coating of the transmitters was particularly appealing to fellow tank-mates and numerous biting attacks were made on the units. This problem was eliminated by camouflaging the transmitters with roofing tar and sand.

The actual attachment was choreographed and refined until it took less than 45 seconds. At dusk, the basking turtle was stealthily approached by one of us and turned over on its back. A short time later, after nightfall, the chosen turtle was propped up at about a 45° angle (head up) while still on its back. Sand was removed to allow room to work under it. A battery-driven drill, equipped with a counterbore bit and a positive stop to limit the depth of the hole was used to make four pilot holes in the carapace. The plastic plate, already equipped with the transmitter, was then screwed into place. The magnet holding the transmitter turned off was removed and a radio check back to the receiving stations was made to ascertain that everything was working. Cold-process roofing tar was applied to the transmitter, plate, and screws and then covered with sand and the turtle righted. The bionic *Chelonia* immediately scrambled to the ocean and swam off and the tracking began (Fig. 3).

The Receivers

We employed two separate receiving stations in order to fix positions of the transmitter-carrying turtles. One was located in the old Coast Guard facility on Tern Island; the other, 13 km away at East Island. Tern Island was the primary receiving station which monitored continuously. The East Island station was only active at 6-hour intervals: 0300, 0900, 1500, and 2100. During that time period bearings were obtained on each of the turtles and their positions plotted.

The receiving equipment at Tern Island consisted of two receiver systems: An omnidirectional antenna connected to a receiver with a frequency scanner and a highly directional antenna connected to a receiver with a signal processor for digital measurements of period and signal strength. The East Island station had a highly directional antenna and a receiver equipped with a processor. The directional antenna at Tern Island (mounted about 9 m off the ground) was positioned with a motorized antenna rotor while the one at East Island (5 m off the ground) was rotated by hand. Bearings were determined from the antenna rotor control box at Tern Island and a compass mounted on the mast at East Island. Under all but the weakest signal conditions, our accuracy of bearing was about ±5°.

In addition to bearing fixes every 6 hours, the station at Tern Island sampled every 10 minutes throughout the whole study period and continuously during three 24-hour periods. The frequency scanner was programmed to scan through the transmitter frequencies. When a signal was detected, the pulse rate was read to determine temperature of the transmitter. These data will be presented in a subsequent paper but it should be mentioned that the amount of time spent on the ocean surface when the signal could be detected was usually less than 1 minute. Thus not much time was available for us to measure pulse rate and fix position.

Every 6 hours the receiving equipment at East Island was turned on. When a turtle signal was detected at Tern Island by the scanner-equipped receiver, the information was relayed to East Island and both stations attempted to fix the bearing of the signal with the directional antennas. Sometimes it was impossible to obtain fixes on all of the turtles. We would hear the signal from a given turtle, but it would not stay on the surface long enough to get an accurate fix.

Residence Times

Four males and four females were equipped with transmitters. For convenience, the turtles were identified by the last three digits of the frequency of their transmitters. For instance, the male equipped with a 149.350 mHz transmitter was known as male 350 (Table 1). This animal was originally tagged with a flipper tag on 31 July 1975 while basking on Whale-Skate Island and recovered on 12 April 1976 and 25 September 1977 while again basking on the same island. The turtle was captured again on Whale-Skate Island and the transmitter attached on 8 June 1980.

Male 540 (149.540 mHz) was originally tagged on 3 May 1979 while basking on Trig Island and found again a day later in the same place. Copulation injuries were noted at the time. The transmitter was attached on 9 June 1980 while on Whale-Skate Island.

Males 360 and 510 had no previous tagging history and had transmitters attached on 8 and 9 June, respectively, while they were on Whale-Skate Island.

Female 200 was originally tagged on 22 March 1968 while basking on Southeast Island, Pearl and Hermes Reef (Fig. 1). The transmitter was attached while the animal was basking on Trig Island 9 June 1980.

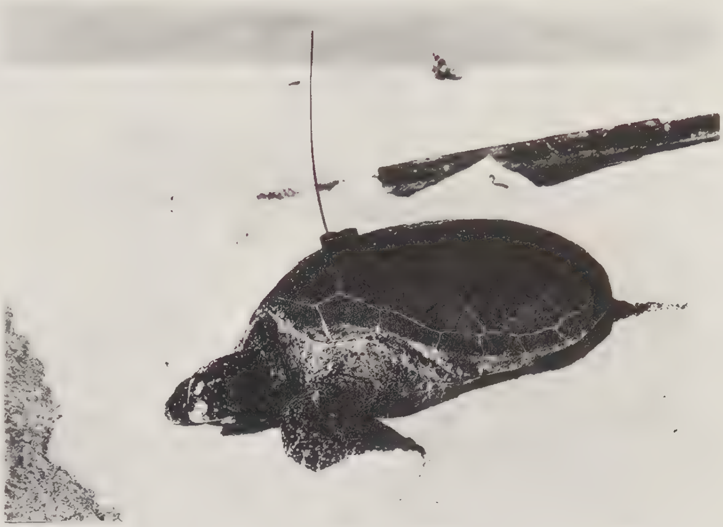

Figure 3.—Transmitter-equipped female 200 returning to the ocean after gear attachment.

Table 1.—Tagging and tracking data. Tagging data are from Balazs' long-term study of the green turtles of Hawaii (Balazs, 1980). The "off" date refers to the date when the last signal was received from the transmitter, WS = Whale-Skate Island, TRIG = Trig Island, and EAST = East Island.

Tagging	First tagging	First recovery	Second recovery	Transmitter deployment		
				On	Off	Days
Male 350						
Date	7/31/75	4/12/76	9/25/77	6/08	9/04	73
Location	WS	WS	WS	WS		
Male 360						
Date	No previous record			6/08	6/27	19
Location				WS		
Male 510						
Date	No previous record			6/09	6/14	5
Location				WS		
Male 540						
Date	5/03/70	5/04/79		6/09	8/12	49
Location	TRIG	TRIG		TRIG		
Female 200						
Date				6/09	6/30	21
Location	3/22/68			TRIG		
Female 450						
Date	7/10/70	7/05/74		6/08	11/13	143
Location	EAST	EAST		WS		
Female 490						
Date	6/19/79	6/29/79		6/09	8/07	60
Location	WS	WS		WS		
Female 530						
Date	No previous record			6/09	8/10	63
Location				TRIG		

[1] Southeast Island, Pearl and Hermes Reef (Fig. 1).

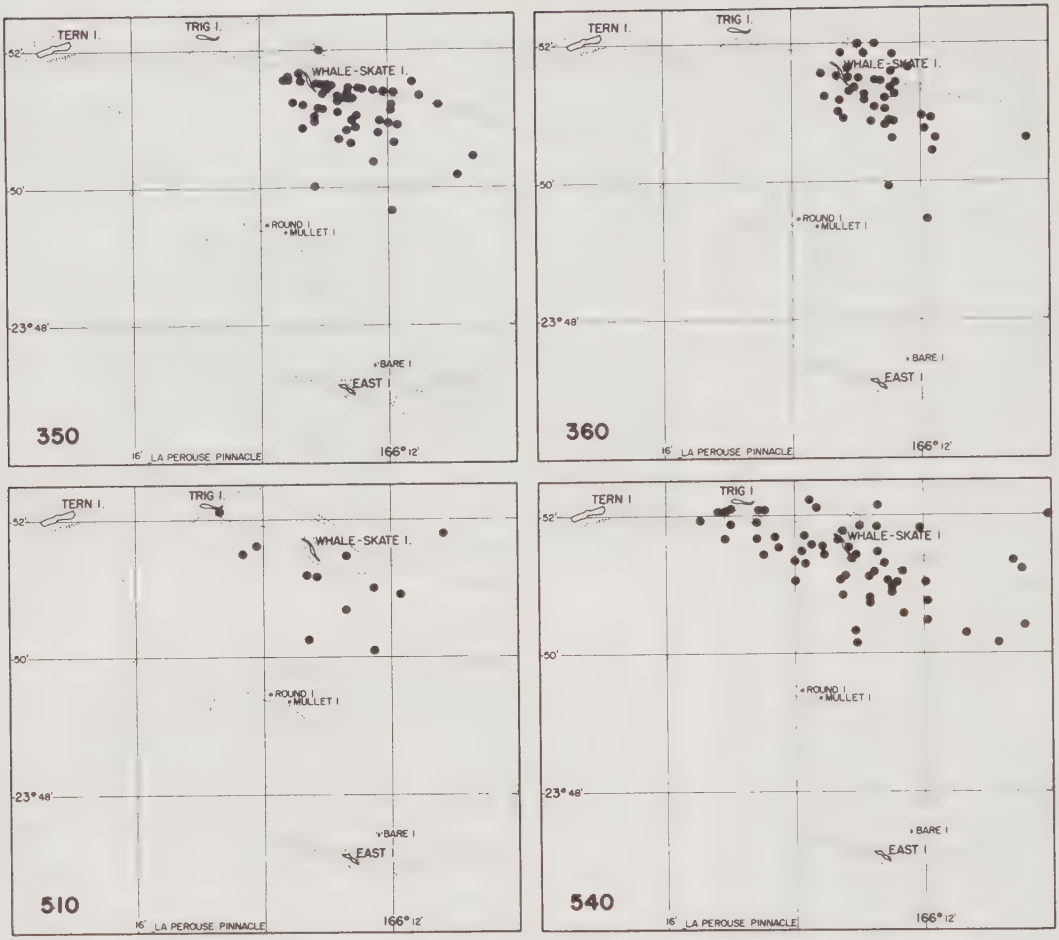

Figure 4.—Distribution of position fixes of the male turtles. Male 510 left the breeding colony about midway into the tracking period.

Female 450 was tagged first on 10 July 1970 and recovered again 5 July 1974 while nesting on East Island. The transmitter was attached on 8 June 1980 while it was basking on Whale-Skate.

Female 490 was first tagged on 19 June 1979 while it was on Whale-Skate and recovered again in the same place 10 days later. The transmitter was attached on 9 June 1980 while it was on Whale-Skate Island.

Female 530 was equipped with the transmitter on 9 June 1980. It had no previous history of tagging.

Our monitoring program was continued until 30 June 1980. Then the station at Tern Island was manned sporadically after our departure by caretaker personnel in order to see how long it was possible to maintain contact with the transmitter-equipped turtles. Of course, when a signal disappeared, it could either mean the turtle departed the colony or had shed the equipment. One transmitter (from female 490) was discovered off Whale-Skate Island in about 2 m of water in June of 1981. The screws were still in the plate and evidenced no sign of corrosion. Female 450 was found nesting on East Island in June 1981 without a transmitter; the small screw holes in the carapace were clean and without any sign of infection. So the attachment method is safe for the turtles and the equipment is eventually shed.

Table 1 also provides information on the length of time signals were heard from the turtles. The signal from male 510 disappeared first. We think it left the breeding colony because its last position was fixed on 14 June far outside the eastern fringing reef. Male 360 was last

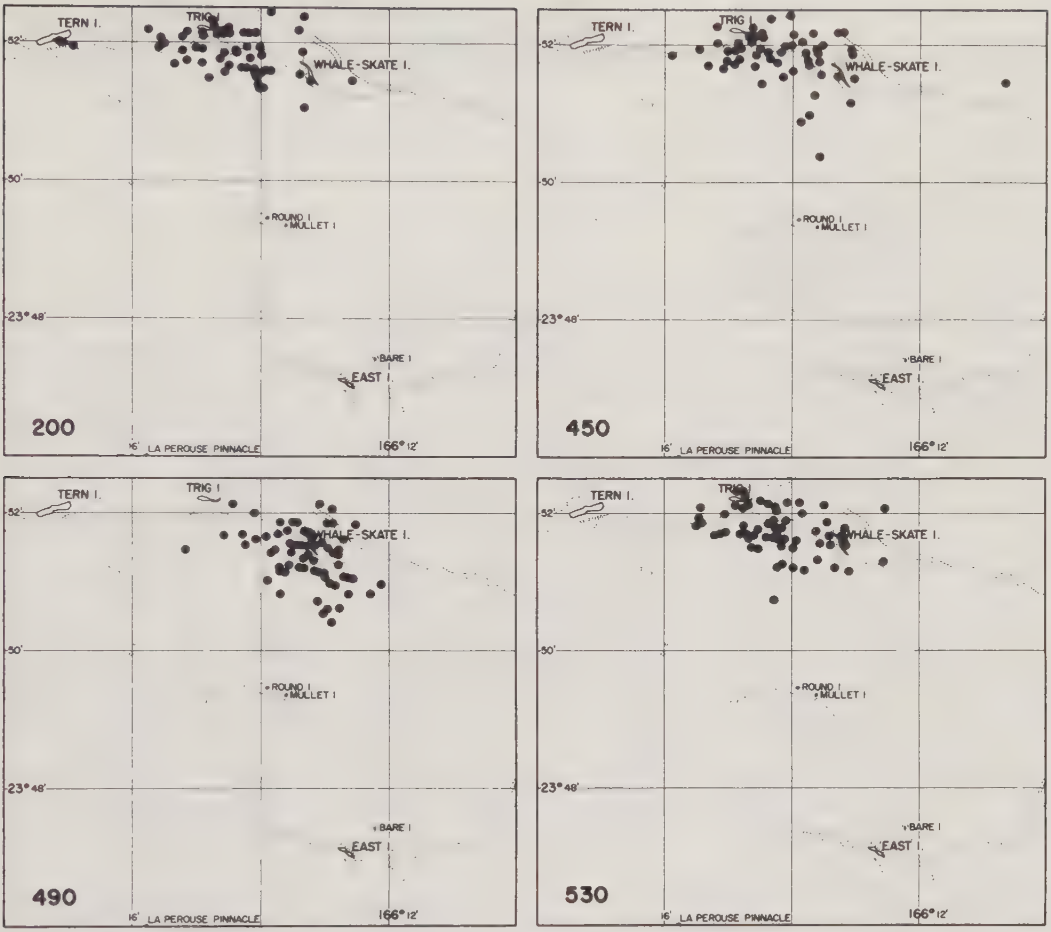
TERN I.
TRIG I
WHALE-SKATE I.
52'
50'
23° 48'
ROUND I
MULLET I
BARE I
EAST I.
200
16'
LA PEROUSE PINNACLE
166° 12'
TERN I.
TRIG I
WHALE-SKATE I.
52'
50'
23° 48'
ROUND I
MULLET I
BARE I
EAST I.
450
16'
LA PEROUSE PINNACLE
166° 12'
TERN I.
TRIG I
WHALE-SKATE I.
52'
50'
23° 48'
ROUND I
MULLET I
BARE I
EAST I.
490
16'
LA PEROUSE PINNACLE
166° 12'
TERN I.
TRIG I
WHALE-SKATE I.
52'
50'
23° 48'
ROUND I
MULLET I
BARE I
EAST I.
530
16'
LA PEROUSE PINNACLE
166° 12'

Figure 5.—Distribution of position fixes of the female turtles. Female 200 regularly came to Tern Island to nest.

heard from on 27 June. Female 200 came to Tern Island to nest twice. At the second nesting we decided to remove the transmitter and evaluate its condition and take a close look at the screw wounds. Both the turtle and the transmitter were fine. Our last transmission from her was on 30 June. She was later spotted again nesting on Tern Island on 17 July.

The other five turtles (350, 450, 490, 530, and 540) were all still transmitting when the field party left Tern Island on 30 June.

Females 490 and 530 remained in the colony until the middle of August, leaving on the 7th and 10th. Male 540 left on the 12th of the same month. Male 350 remained another month and was last heard from on 4 September. Female 450 remained the longest in the breeding colony (signals were heard until 13 November). She is likely a permanent resident of FFS.

Habitat Utilized

Our results show that the nearshore habitat of males and females at the breeding colony is in proximity to the basking and nesting islands near where they were captured (Fig. 4, 5). While understandable perhaps for the females, it is curious that the males adhere so closely to the nesting beaches. East Island remains the nesting site for 55 percent of the FFS-breeding turtles. Nevertheless we never observed our turtles traveling the 9 km south to the East Island area. Clearly, there is a strong evolutionary bias for a female to return to the same nesting beach year after year. Since the beach was adequate for her mother and for her as a hatchling, it is highly probable it will be adequate for her and for her hatchlings. But the males have no such stake. The best strategy would be to impregnate as many females as possible regardless of which nesting beach they will eventually employ. Thus it is curious that the ranges of the males were so tightly coupled to the place they were tagged. This specificity apparently extends over the years. Male 350 was originally tagged on Whale-Skate Island in 1975 and male 540 was tagged in 1979 on Trig Island. Table 2 details previous records of year-to-year visits by males and females to the various islands. The approximately 13-20 percent straying could be due at least in part to the permanent residents. They seem, as female 450 shows, to make use of more of the reefs and beaches of FFS. She was heard from well into November and was spotted several times on the beach at East Island during the summer of 1981.

Table 2.—Specificity of returns by male and female turtles to listed areas within the French Frigate Shoals breeding grounds (Balazs, 1980). Data are based upon a tagging and subsequent recoveries from 1970 to 1980. TRIG-WS = Trig Island and Whale-Skate Island complex, EAST = East Island, and GIN = Gin Island complex (Fig. 1).

Item	TRIG-WS same/stray	EAST same/stray	GIN same/stray	Total same/stray
Males				
Number	33/8	16/2	0/0	49/10
Percent stray	24	12	—	20
Females				
Number	15/5	68/3	0/3	83/11
Percent stray	33	4	100	13

Thus, our results strongly infer that imprinting to the nesting beach and its environs occurs in both males and females and that this response seems permanent at least over several years. These results also emphasize the importance of maintaining the utilized marine habitat and the nesting beach as free from disturbing influences as possible. It is imperative for the well-being of the population that no alterations in the habitat be made since once imprinted the green turtle is unlikely to switch its breeding habitat.

Acknowledgments

Our telemetry field team also included Causey Whittow, Howard A. Jemison III, Steven Kramer, Susan and Robert Schulmeister, Ruth Ittner, and Elizabeth Flint. Each of these individuals made valuable contributions to the project. We also want to express our appreciation to the U.S. Fish and Wildlife Service for the use of support facilities on Tern Island, and for permitting the research to be conducted within the Hawaiian Islands National Wildlife Refuge.

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BIOENERGETICS AND GROWTH OF STRIPED BASS, *MORONE SAXATILIS*, EMBRYOS AND LARVAE

MAXWELL B. ELDRIDGE, JEANNETTE A. WHIPPLE, AND MICHAEL J. BOWERS[1]

ABSTRACT

Fluctuations in year class size of striped bass are known to be related to development and survival in the early life stages. Bioenergetic aspects of growth and development of striped bass embryos and larvae were determined in the laboratory to discover some of the physiological needs and processes of these stages from fertilization to metamorphosis.

Energy was provided by endogenous (yolk and oil globule) and exogenous (*Artemia* sp.) sources. Initial amounts of yolk and oil varied significantly among eggs from seven different females, and these differences were reflected in different patterns of consumption and growth. Feeding larvae consumed their endogenous oil at rates related to exogenous food intake. Daily food rations of larvae from the onset of feeding to metamorphosis were estimated for field and laboratory conditions. Rations increased with size and age of the larvae. Wild larvae were estimated to have daily rations substantially greater than those of cultured larvae.

Energy outputs were measured in growth and oxygen consumption. Egg size (total dry weight) directly influenced early periods of growth, but later compensatory growth, seen in more rapid growth in larvae from smaller eggs, made up for initial differences. Growth and food consumption were linearly related and, again, different growth characteristics were seen in each batch of fish. Embryos and prefeeding larvae had the highest Q_{O_2}, while metabolism on a weight-specific basis increased with tissue dry weight and was best described by a power function.

Gross caloric conversion efficiencies were highest from fertilization to initial feeding. Feeding larvae used their resources at levels under 20% and their conversion efficiencies did not appear to correlate with food concentration.

In an energy budget model, striped bass embryos and larvae given the highest food density consumed yolk energy at constant rates until totally absorbed. Oil globule consumption fluctuated in relation to growth and nonassimilation, rising sharply after first feeding then declining as food intake increased. Metabolism fluctuated according to developmental stage, rising with the onset of active feeding. Nonassimilation steadily increased as larvae relied more on exogenous food.

Striped bass, *Morone saxatilis*, populations have fluctuated historically throughout their ranges, but in recent years they have declined consistently and unexplainably, especially on the west coast of the United States. Present estimates place the population of the San Francisco Bay/Delta estuary at 33% to 40% of its 1960 peak abundance and it is forecasted to decline further (Stevens 1980). Despite availability of considerable information on striped bass (Pfuderer et al. 1975; Rogers and Westin 1975; Horseman and Kernehan 1976; Setzler et al. 1980), factors that control or influence these fluctuations and declines are not known. Field researchers concluded from 20 yr of data collection that year class size directly correlates with survival and growth during the first 60 d of life and this, in turn, is controlled by environmental conditions—principally the interrelated factors of freshwater flow, water diversion, and food supply (Stevens 1977a, b; Chadwick 1979[2]; Stevens 1980).

To determine the direct causal mechanisms operating between these environmental conditions and early life stage growth and survival, we conducted a series of laboratory experiments over a 6-yr period. Our working hypothesis was that a combination of inherent and environmental factors determined the ability of striped bass embryos and larvae to meet metabolic requirements for successful growth and survival to the pivotal age of 60 d. These factors involve a variety of physiological, morphological, and behavioral functions, and are controlled and/or limited by environmental conditions. Whole organism

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[1] Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

[2] Chadwick, H. K. 1979. Striped bass in California. Prepared for U.S. Environmental Protection Agency, Region II, 27 p.

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FISHERY BULLETIN: VOL. 80, NO. 3, 1982.

bioenergetics was selected as our approach because it represents these functions in an integrated and comprehensive fashion.

Bioenergetics of adult fishes has been studied for some time (Ivlev 1939a, b; Winberg 1956; Warren and Davis 1967; Brett and Groves 1979). As interest in fish eggs and larvae grew, knowledge gained from studies of adults was applied toward research on early life stage energetics (Toetz 1966; Laurence 1969, 1971, 1977; Cooney 1973). Most of these publications are concerned with the critical period when larvae begin active feeding and change from endogenous to exogenous energy sources (May 1974b). Other researchers have used bioenergetic studies to assess the effects of pollutants or other environmental conditions on larvae (Laurence 1973; Eldridge et al. 1977).

Our early research on striped bass embryos and larvae has already been reported (Eldridge et al. 1981). Emphasis was on factors associated with food and feeding of larvae and how they related to mortality, point of no return, development, and, to a limited extent, energetics. The research presented here is a detailed analysis of the energy sources, endogenous and exogenous, and their influence on energy outputs in the early life stages of striped bass.

MATERIALS AND METHODS

Energy Input Determinations

Component analyses of eggs prior to fertilization were done on eggs from seven different females used for embryo and larval studies and on 34 ripe fish collected at random from natural spawning areas. All eggs came from fish from the Sacramento River, Calif. Three replicates of 25 eggs each were weighed fresh after brief blotting on absorbent filter paper, then dried to constant weights at 60°C and reweighed to yield water contents and total dry weights. Yolks and chorions were dissected from Formalin[3]-preserved eggs with microdissection tools; they then were dried and weighed to the nearest 0.1 μg. These amounts were then subtracted from the total weight to provide oil weights. Total lipid contents were obtained by 2:1 chloroform-methanol extraction in micro-Sohxlet apparatus. Our procedure for caloric determinations of yolk and oil involved whole egg homogenization followed by centrifugation to separate yolk, oil, and chorion membrane components. Yolk and oil were then aspirated into dishes, oven dried to constant weights at 60°C, and bombed according to standard microbomb calorimetric methods. Estimates of tissue and *Artemia* caloric contents were made from homogenates of whole animals, the larvae being sampled after complete oil globule consumption. All caloric contents are expressed as calories per gram ash-free dry weight.

All measurements of yolk and oil volume and lengths were done with ocular micrometers in dissecting microscopes. All measurements and determinations were performed at least in duplicate and, if possible, in triplicate.

Eggs from seven different females were fertilized artificially according to methods of Bonn et al. (1976). Eggs were incubated in McDonald jars. After hatching, larvae were transferred to hemispherical 8 l acrylic plastic containers held in water tables to stabilize temperature. Initial stocking densities were approximately 150 larvae/container. In three of the seven batches, larvae were reared to the age when feeding begins, 7 d after fertilization (D-7). The remaining four batches were reared to 29 d after fertilization (D-29). During the process we attempted to duplicate natural water quality conditions as much as possible. Temperatures were maintained at 18°C, and oxygen content was at or near saturation throughout the experiments. Photoperiod and light qualities were kept close to natural. Salinities were zero from fertilization to D-4, 1.0‰ from D-5 to D-13, and 3‰ from D-14 to D-29. Each day containers were cleaned and new water and food were added. An endemic small (1-2 μm) green phytoplankter (*Nephroselmus* sp.) was also added in concentrations of 10^2-10^3/ml.

Larvae began feeding consistently on D-7, at which time they were given newly hatched, live *Artemia salina* nauplii (San Francisco Bay Brand). The range of initial food concentrations was selected to include the estimated natural zooplankton densities (0.003 to 0.010/ml (Daniel 1976)) and the concentrations used in other striped bass research. Initial concentrations were 0.00, 0.01, 0.10, 0.50, 1.00, and 5.00 *Artemia*/ml.

To estimate daily exogenous food rations of larvae we used the following formula: daily food ration = (average stomach contents)(hours of active feeding)/digestive time. Detailed studies on diel feeding patterns and evacuation rates of larvae in our experimental systems were conducted in the early stages of this study and were presented in Eldridge et al. (1981). Because larvae in all food concentrations consumed their food within 10 h after food was first introduced, we selected 10 h/d for use in the above formula. We found that sampling larval stomachs 1 h after food introduction was most representative of average stomach contents during the active feeding periods. A minimum of 10 larvae was dissected and the stomach contents were quantified for each food ration estimate for each experiment. Evacuation rates of food ingested by larvae which were feeding continuously ranged from 1.5 to 5.5 h with an overall average of 3.3 h. Times of 100% evacuation were combined for different-aged larvae and used in this study (Table 1).

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Average times (h) required for *Artemia* nauplii to pass through the digestive tracts of continuously feeding striped bass larvae.

Age (days after fertilization)	Food concentration (*Artemia*/ml)				
	0.01	0.10	0.50	1.00	5.00
9-16	3.3	4.0	3.5	4.5	4.0
17-24	2.5	2.8	3.5	3.5	2.3
25-29	2.5	2.5	3.7	4.0	3.0

Energy Output Determinations

Growth of embryos and larvae was measured by carefully removing all yolk and oil globules from Formalin-preserved specimens, rinsing the remaining tissues in distilled water, drying at 60°C, and weighing to the nearest 0.1 μg. Measurements were in duplicate with 3 to 5 specimens per sample. Standard lengths of larvae were measured to the nearest 0.1 mm with an ocular micrometer. Duplicate measurements of 20 larvae each were done. Preserved specimens were measured as soon as possible. The entire set of samples from each experiment required an average of 8 wk to process.

Oxygen consumption was used as a measure of "routine" metabolism (Fry 1971) and was measured with standard manometric techniques using a differential microrespirometer. At least five replicate samples (from 5 to 50 animals/sample depending on age and size) were taken at each test period. Sampling occurred at D-0.5, -1.0, -2.0, -4.0, and on each even day until D-30 (time measured from time of fertilization).

RESULTS

Energy Inputs

Endogenous Sources

Initial sources of energy for striped bass embryos and early larvae are yolk and oil, the latter contained in a single large globule. The relative composition of these egg components was found to vary considerably between the seven different females used in rearing experiments (Table 2). Oil accounts for most of the variability in dry weight, whereas yolk is more variable in measurements of volume. Caloric contents of these two energy sources were consistent, which indicates that variability of total energy in the egg results from differences in absolute amounts of oil, yolk, or both, rather than differences in the energy content of those materials. Eggs from different females contained widely ranging

TABLE 2.—Dry weights, volumes, and caloric contents of striped bass eggs and egg components at time of fertilization. Three replicates of 25 eggs each were used for dry weights, three replicates of 20 eggs each for volumes, and two replicates of approximately 50 mg (dry weight) were used for caloric content determinations.

Experiment no.	Mean dry weight (mg)				Mean volume (mm^3)		Caloric content				
							yolk		oil		total
	yolk	oil	chorion	total	yolk	oil	cal/g	cal/egg	cal/g	cal/egg	cal/egg
1	0.114	0.150	0.022	0.286	0.67	0.21	5,687	0.648	9,223	1.383	2.031
2	0.089	0.137	0.023	0.249	0.65	0.20	5,720	0.509	9,360	1.282	1.791
3	0.131	0.089	0.028	0.248	0.57	0.13	5,622	0.736	9,133	0.813	1.549
4	0.106	0.251	0.016	0.373	0.52	0.21	5,641	0.596	9,869	2.477	3.073
5	0.118	0.189	0.014	0.321	0.20	0.17	5,635	0.665	9,627	1.819	2.484
6	0.089	0.128	0.014	0.231	0.38	0.18	5,635	0.502	9,738	1.247	1.749
7	0.083	0.115	0.012	0.210	0.62	0.14	5,625	0.467	9,655	1.110	1.577
$\bar{x}$	0.104	0.151	0.018	0.274	0.516	0.177	5,652	0.589	9,515	1.447	2.036
SE	0.018	0.054	0.006	0.057	0.170	0.033	37	0.100	278	0.546	0.558
Range	0.089– 0.131	0.089– 0.251	0.012– 0.028	0.210– 0.373	0.20– 0.67	0.13– 0.21	5,641– 5,720	0.467– 0.736	9,133– 9,869	0.813– 2.477	1.549– 3.037
C.V.	17.3	35.6	33.0	20.8	33.0	18.4	0.7	16.9	2.9	37.7	27.4

amounts of yolk and oil (coefficients of variation 27% and 25% for yolk and oil, respectively) and little (<3%) difference was found in energy contents. The oil globule accounted for an average 55% of the dry weight and 71% of the total energy of the egg. Yolk accounted for 38% of dry weight and 29% of energy. The two sources combined provided an average 2.036 cal/egg.

Yolk contained an average 5,652 cal/g, which agrees with Phillips' (1969) estimate of 5,660 cal/g gross energy for digested protein. Lipid extraction analyses of yolk from three of the seven spawned females showed that only 3.8% of dry weight was lipid material.

Embryos and larvae from the seven different females consumed their yolks linearly (Fig. 1). At hatching an average 58% of the original yolk energies remained, and they were totally utilized between D-6 and D-7, the time when active feeding began. Analyses showed no significant differences in yolk utilization rates but highly significant differences in intercepts ($P \leq 0.01$), further indication of the differences in original yolk reserves.

Initial oil energy contents per egg ranged from 0.8 to 2.5 cal (Table 2) and differed significantly between batches ($P \leq 0.05$). An average 86% of these initial amounts remained at hatching and 71% was present on D-7. Analyses of covariance indicated that the utilization rates from fertilization to feeding (Fig. 2) also were significantly different ($P \leq 0.05$). With the exception of one batch, embryos and larvae consumed their oil energies so that approximately the same amounts of energy remained on D-7.

The rates at which oil globule calories were utilized and the ages at complete oil energy absorption (D-20 to D-29) appeared related to food concentration (Fig. 3). Starved larvae and those in 0.01 *Artemia*/ml concentrations conserved oil, whereas those fed progressively higher concentrations consumed energy at faster rates. Analyses of covariance showed significant differences in oil consumption among batches within each food concentration. Tests of food concentrations and oil consumption within batches showed all to have highly significant differences ($P \leq 0.01$) in intercepts, and two of the four batches had significant slope differences ($P \leq 0.05$).

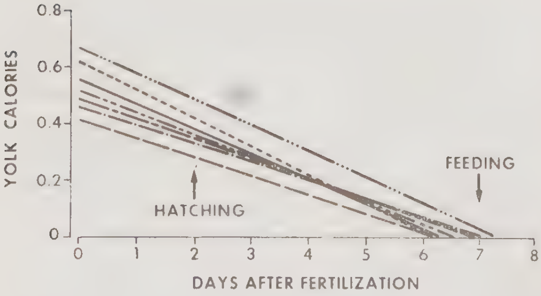

FIGURE 1.—The consumption of yolk calories by seven different batches of striped bass embryos and larvae cultured under identical conditions.

Exogenous Sources

Larvae in all experiments began active feeding 5 d after hatching. Average stomach contents, presented as the average number of ingested *Artemia* and their equivalent calories, are presented in Table 3. These data were further used to calculate daily food rations (Table 4). With some exceptions, larvae increased their exogenous energy intake in direct relation to food availability and age in all food concentrations except 0.01 *Artemia*/ml. Larvae in this low concentration showed no particular trend.

Energy Outputs

Growth

Embryonic and prefeeding larval growth, measured in assimilated tissue calories, differed significantly among the seven batches ($P \leq 0.01$).

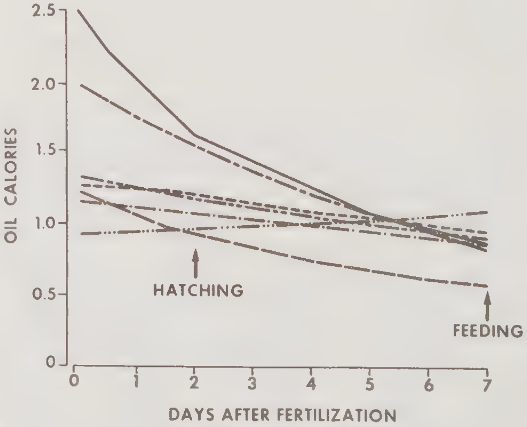

FIGURE 2.—The consumption of oil globule calories by seven different batches of striped bass embryos and prefeeding larvae.

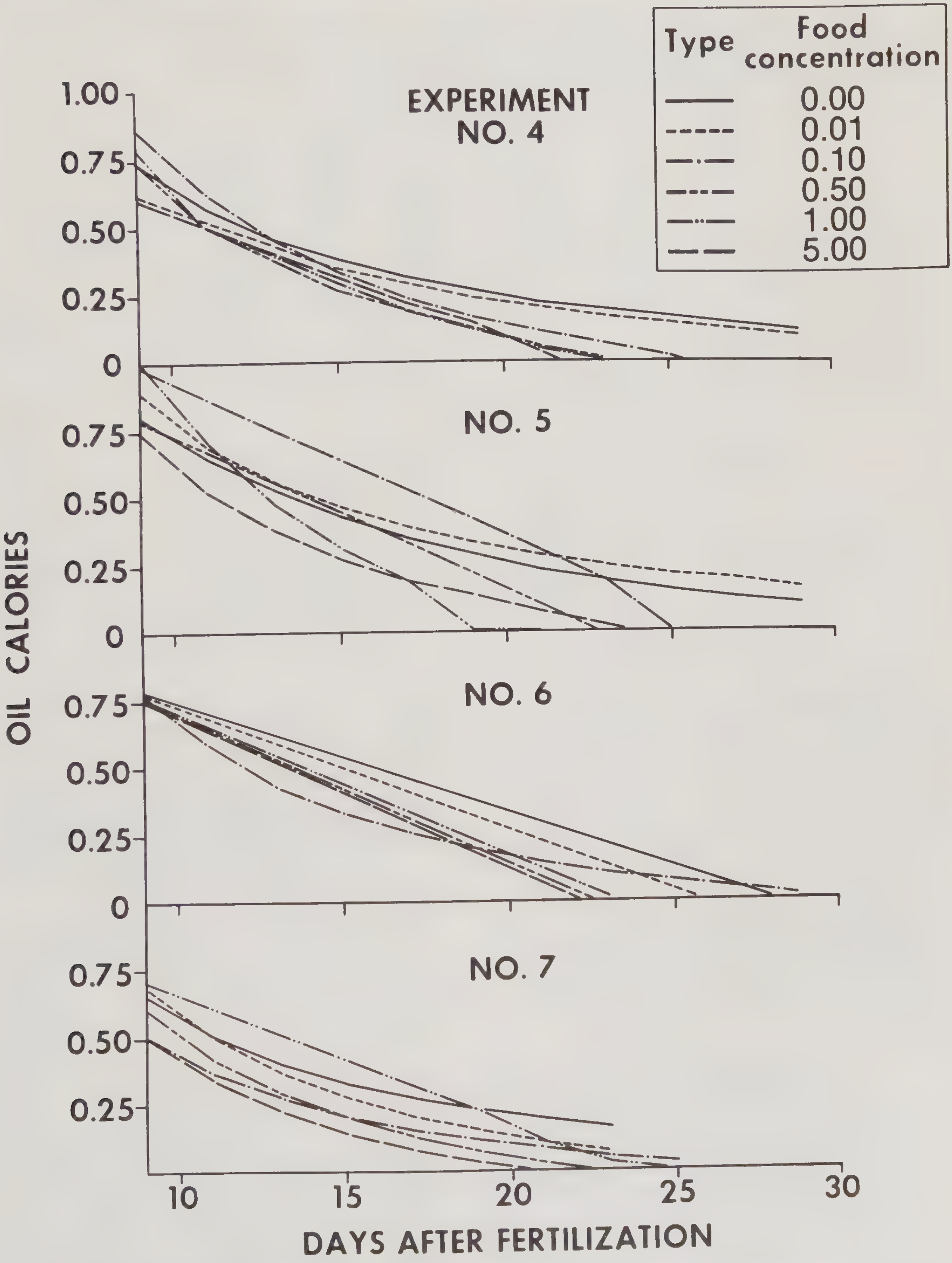

FIGURE 3.—The consumption of oil globule calories by striped bass larvae from four different batches (experiments 4-7) fed six different food concentrations (0.00 to 5.00 *Artemia*/ml).

TABLE 3.—Average stomach contents and their corresponding caloric equivalents of striped bass larvae feeding at different food concentrations from 9 to 29 d after fertilization. Presented as number of food organisms/number of calories per larva.

Age (days after fertilization)	Food concentrations (no. *Artemia*/ml)				
	0.01	0.10	0.50	1.00	5.00
9	0.05/0.001	0.15/0.001	5.40/0.052	4.30/0.041	7.60/0.073
11	0/0	0.85/0.008	7.50/0.072	11.70/0.112	2.80/0.027
13	1.50/0.014	3.30/0.032	9.20/0.088	18.40/0.177	9.890/0.094
15	0.05/0.001	4.10/0.039	23.10/0.222	24.00/0.231	10.20/0.098
17	0.15/0.001	8.40/0.081	27.10/0.260	39.40/0.39	18.60/0.179
19	0/0	12.50/0.120	29.50/0.283	33.30/0.320	24.60/0.236
21	0.15/0.001	13.00/0.125	26.10/0.251	40.00/0.384	33.70/0.324
23	4.16/0.040	14.20/0.136	47.40/0.456	35.90/0.345	53.00/0.509
25	1.10/0.001	57.20/0.550	17.00/0.163	83.10/0.799	59.40/0.571
27	0.25/0.002	470/0.045	65.40/0.628	60.20/0.579	72.40/0.696

TABLE 4.—Estimated daily food ration (number of *Artemia* consumed by one larva in 24 h/equivalent calories consumed in 24 h) of striped bass larvae at different ages feeding at different food densities.

Age (days after fertilization)	Prey densities (*Artemia*/ml)				
	0.01	0.10	0.50	1.00	5.00
9	0.2/0.001	0.4/0.004	15.4/0.148	9.6/0.092	19.0/0.183
11	0/0	2.1/0.020	21.4/0.206	26.0/0.250	7.0/0.067
13	4.6/0.044	8.3/0.079	26.3/0.253	40.9/0.393	24.5/0.235
15	0.2/0.001	10.3/0.099	66.0/0.634	53.3/0.513	25.5/0.245
17	0.6/0.006	30.5/0.294	77.4/0.744	112.6/1.082	82.7/0.794
19	0/0	45.5/0.437	84.3/0.810	95.1/0.914	109.3/1.051
21	0.6/0.006	47.3/0.454	74.6/0.717	114.3/1.098	149.8/1.439
23	16.6/0.160	51.6/0.496	135.4/1.301	102.6/0.986	235.6/2.264
25	1.0/0.010	18.8/0.181	176.8/1.699	150.5/1.446	241.3/2.319
29	11.6/0.111	58.8/0.565	194.3/1.867	288.8/2.775	410.0/3.940

Greater differences were seen in the intercepts than rates, and this, in turn, seemed related to the initial egg sizes (total dry weights). Descriptive equations for assimilated tissue calories of the different experiments are in Table 5. Daily growth coefficients (Laurence 1974) to hatching and to first feeding correlated well with initial egg size. The rate of growth from fertilization to hatching age (avg. $G_W = 1.872$) was three times that to feeding age (avg. $G_W = 0.647$).

Standard lengths at hatching (3.9±0.6 mm), and especially at first feeding (5.8±0.3 mm) (Table 5), also correlated well with initial egg size. Smaller standard deviation of D-7 larvae than of newly hatched larvae (coefficients of variation 5% vs. 15%) suggests larval lengths converged with age.

Growth characteristics of feeding larvae were unique to each batch within each food concentration as was found in earlier stages. Examples are given in Figures 4 and 5 which present growth in tissue calories and standard lengths of larvae fed the high food ration (5.0 *Artemia*/ml).

Within each batch, growth was linearly related to food concentration (Fig. 6). Differences in overall growth are again apparent. Experiment 7 larvae grew fastest.

Larval length-weight relations were exponen-

TABLE 5.—Best descriptive equations (y = tissue calories, x = days after fertilization), initial egg dry weights, standard length, and growth coefficients of striped bass embryos and prefeeding larvae.

Experiment	Initial egg size (μg)	Best fit growth equation (tissue cal)	Standard errors of estimate	Standard lengths (mm)		Daily instantaneous growth coefficients[1]	
				at hatching	at feeding	to hatching	to feeding
1	286	$y = 0.159359\ (x^{0.578582})$	0.0480	4.7	5.5	1.966	0.624
2	249	$y = 0.107496\ (x^{0.847936})$	0.0653	4.0	5.6	1.844	0.630
3	248	$y = 0.133695\ (x^{0.860384})$	0.0446	4.7	5.7	1.733	0.694
4	373	$y = 0.139619\ (x^{0.732174})$	0.0537	3.2	6.1	2.172	0.715
5	321	$y = 0.190165\ (x^{0.767811})$	0.0537	3.2	6.1	2.172	0.715
6	231	$y = 0.090892\ (x^{0.828653})$	0.0187	3.6	5.9	1.763	0.633
7	210	$y = 0.115968\ (x^{0.692893})$	0.0763	3.7	5.4	1.733	0.580

[1] Daily instantaneous growth coefficients = $\log_e W$/days after fertilization where W = dissected tissue dry weight in micrograms.

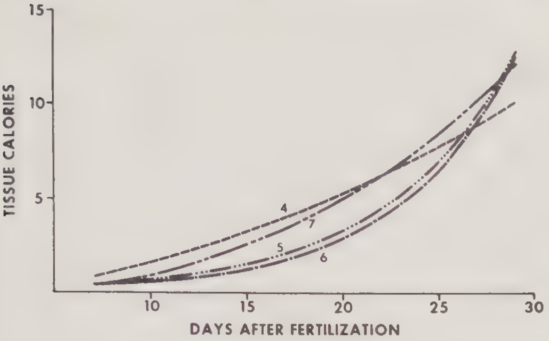

FIGURE 4.—Growth of four batches of feeding striped bass larvae measured in calories of assimilated tissue from first feeding (D-7) to D-29.

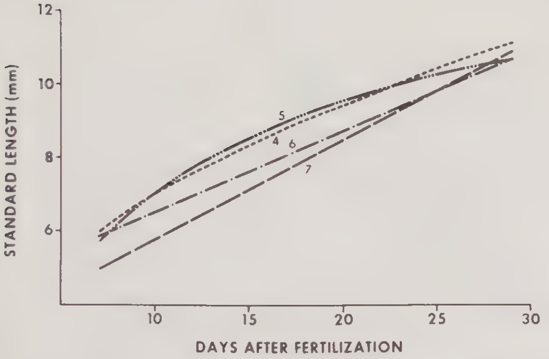

FIGURE 5.—Growth of four batches of feeding striped bass larvae measured in standard lengths from first feeding (D-7) to D-29.

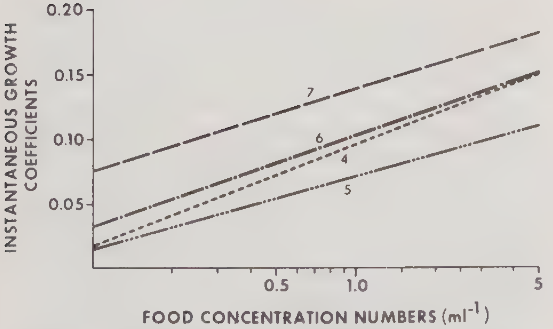

FIGURE 6.—Instantaneous growth coefficients of four batches of feeding striped bass larvae that fed on six different food concentrations (0.00 to 5.00 *Artemia*/ml).

tial for all fish groups (Fig. 7). Experiment 7 larvae were the heaviest per unit length and did not attain the lengths that other larvae did. All larvae put on weight rapidly after reaching a standard length of about 8 mm.

Oxygen Consumption

Metabolic rates of embryos and larvae are presented in Figure 8. Embryos and prefeeding larvae had the highest Q_{O_2}'s. After feeding began oxygen consumption stabilized and remained constant for the duration of the experimental period. On a weight-specific basis oxygen consumption increased with tissue dry weight and was best described by a power function (Fig. 8), although the relationship appears almost linear.

Utilization Efficiency

Gross caloric conversion efficiencies were highest from fertilization to initial feeding, followed closely by efficiencies during the embryonic period (Table 6). Only in larvae from the highest food concentration did conversion efficiencies remain at elevated levels. Larvae feeding at the other food concentrations used their resources at levels under 20%, and their conversion efficiencies did not appear to correlate with food concentration. Starved larvae had the lowest efficiency and demonstrated negligible growth after D-7.

TABLE 6.—Mean gross caloric conversion efficiencies (in percent) for striped bass embryos, prefeeding larvae, and larvae feeding at different prey concentrations.

To hatching	To initial feeding	Food concentrations (*Artemia*/ml) to 29 d after fertilization					
		0.00	0.01	0.10	0.50	1.00	5.00
37.7	43.8	15.0	19.0	13.9	17.3	18.7	31.9

DISCUSSION

Energy Inputs

Striped bass eggs were found to be high in energy content and to vary considerably in size. Undoubtedly the high proportion of lipids (found mostly in the oil globule) makes the striped bass egg one of the most energy-rich of fish eggs. At 7,808 cal/g striped bass eggs exceed the caloric values of eggs from freshwater, anadromous, and marine fishes which normally range from 5,386 to 6,238 cal/g (Hayes 1949; Smith 1957,

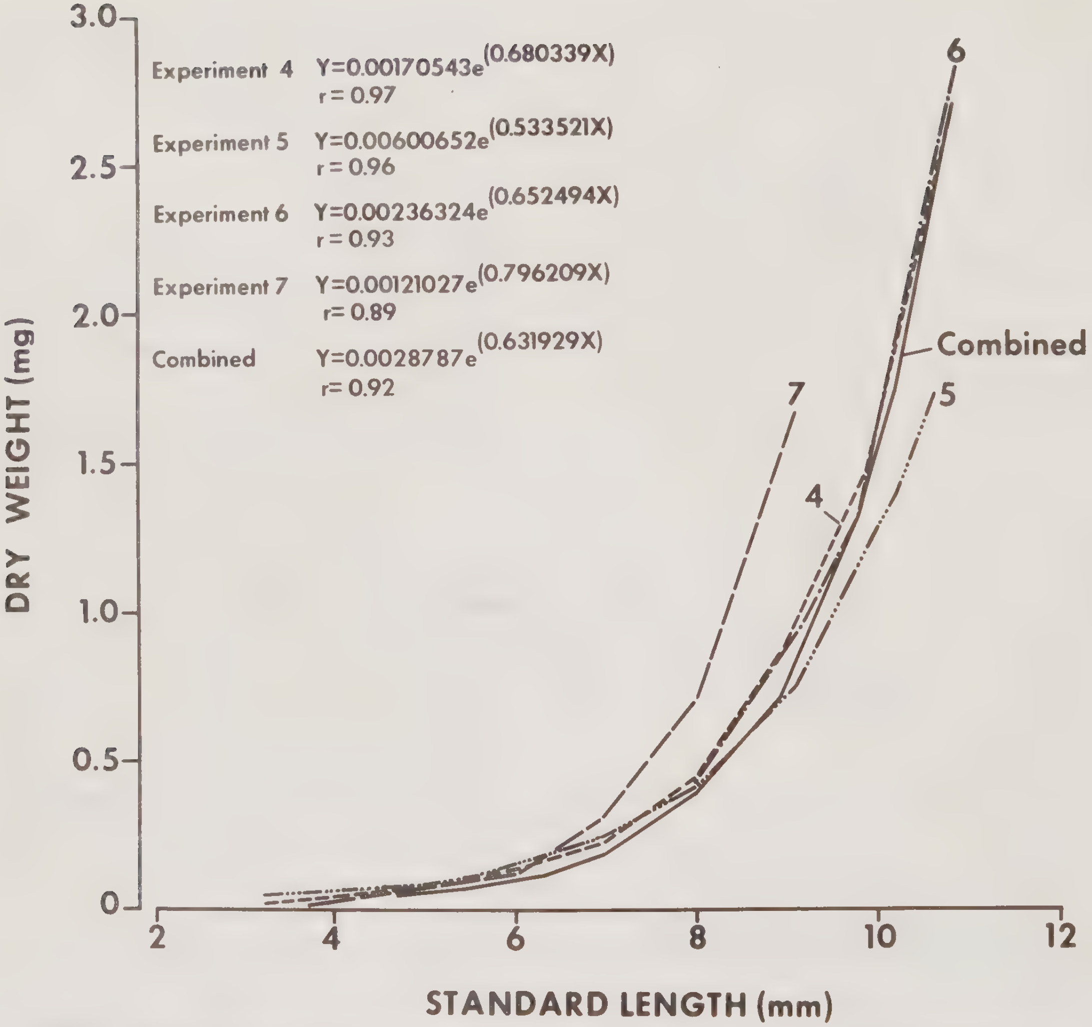

FIGURE 7.—Assimilated tissue dry weights and corresponding standard lengths of four batches of striped bass larvae.

1958; Flüchter and Pandian 1968; Blaxter 1969). Egg size variability was not unexpected as eggs are reported to vary within and among a variety of fish species (*Clupea harengus*, Blaxter and Hempel 1963; *Sardinops caerulea*, Lasker 1962; *Trachurius symmetricus*, Ware 1975; Theilacker 1980[4]).

It appears from studies of embryos and larvae with large oil globules that the energy from the oil is important to larval growth and survival, and the influence of this energy source is present for long periods. In this study and that of Rogers and Westin (1981), striped bass larvae retained their oil energy reserves for extended periods, especially when starved. This is not common in fishes although similar retention of the oil globule was noted in *Bairdiella icistia* (May 1974a) and *Leuresthes tenuis* (May 1971; Ehrlich and Muszuski in press). The oil globule also seemed to help striped bass larvae avoid or prolong the typical point-of-no-return, the time of irreversible starvation (Eldridge et al. 1981). In a review of larval fish physiology, Theilacker (1980) concluded that in addition to egg size and activity, egg lipid level relates most to larval resilience.

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[4] Theilacker, G. H. 1980. A review of pelagic larval fish behavior and physiology. Presented at Institute del Mar del Peeru (IMARPE) Workshop, April 21-May 5, 1980.

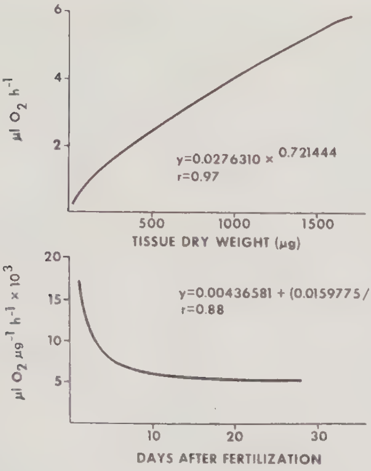

FIGURE 8.—Oxygen consumption of striped bass embryos and larvae plotted against assimilated tissue dry weight (above) and age (below).

In an attempt to compare our laboratory derived estimates of daily food ration with those from wild striped bass larvae we obtained stomach content data of 1,468 field-caught larvae (sized to 11.9 mm SL) spawned from 1971 to 1973. The summarized data of Table 7 show wild larvae were smaller (4.0 to 4.9 mm) than laboratory larvae (6.1 mm) at the time of first feeding. This is possibly due to differences in preservation methods. When wild larvae attained sizes of 7.0 to 7.9 mm, over 75% were feeding. This agrees with our laboratory observation that over 80% of the 2-wk-old and older larvae (>7.0 mm SL) fed actively in food concentrations of 0.50 *Artemia*/ml and greater. The overall average of feeding incidence for wild larvae was 70.5%. Wild larvae also displayed preference for cladocerans, *Cyclops* sp. and *Eurytemora* sp., which, together, accounted for 89% of all food consumed. Other studies of striped bass from east coast nursery areas showed that the largest part of the larval diet consisted of small crustacea and microplankton (Meshaw 1969; Humphries and Cumming 1972).

Using these data we calculated daily caloric rations, according to the previously described formula, for each size category of wild larvae (Table 7). Caloric equivalences for the different food types were obtained from the literature (Richman 1958; Cummins 1967; Clutter and Theilacker 1971; Laurence 1976; Sitts 1978). In-

TABLE 7.—Average feeding incidences, stomach contents by food item, equivalent caloric values, and calculated daily caloric rations of 1,468 striped bass larvae collected in the San Francisco Bay/Delta estuary during 1971-73. The last column presents laboratory-derived average caloric rations for larvae of comparable sizes.

Larval size (mm SL)	% with food in stomachs	Neomysis	Corophium	Cladocerans	Cyclops	Diaptomus	Eurytemora	Acartia	Harpacticoids	Misc. copepods	Total caloric equivalent	Estimated daily ration (cal)	Laboratory derived average ration (cal)
3.0-3.9	0	0	0	0	0	0	0	0	0	0	0		—
4.0-4.9	16.1	0	0.01	0.29	0.18	0	0.24	0.01	0.03	0.01	0.107	0.646	—
5.0-5.9	32.6	0.02	0.09	0.82	0.60	0	0.28	0.01	0.01	0.01	0.299	1.801	—
6.0-6.9	57.5	0	0.10	0.80	0.81	0.01	0.38	0.01	0.01	0.01	0.317	1.910	0.183
7.0-7.9	76.7	0.02	0.11	0.82	1.00	0.01	0.49	0.01	0.02	0.01	0.357	2.152	0.151
8.0-8.9	80.9	0.04	0.14	0.97	1.22	0.01	0.63	0.01	0.02	0.01	0.436	2.627	0.520
9.0-9.9	84.7	0.09	0.18	1.08	1.25	0.01	0.68	0.01	0.03	0.02	0.496	2.989	1.245
10.0-10.9	85.3	0.16	0.22	1.31	1.27	0.04	0.82	0.01	0.01	0.02	0.599	3.609	2.607
11.0-11.9	82.9	0.19	0.28	1.51	1.37	0.02	0.92	0.01	0.02	0.01	0.689	4.151	N/A

formation on natural feeding duration was taken from Miller,[5] which showed that wild larvae feed 24 h a day but feed more intensely during crepuscular periods. Evacuation rate was set at 5 h, a compromise between our estimate of 3.3 h for larvae fed *Artemia* at 18°C and the estimate of 11 to 12 h made by McHugh and Heidinger (1977) for larvae given *Artemia* and held at 25°C. Daily caloric rations for wild larvae range from 0.646 cal for smaller larvae to 4.151 cal for 11.0 to 11.9 mm SL larvae. These rations are higher than those of laboratory larvae. Except for the largest cultured larvae, rations were usually one-half the field larvae rations. Thus within equivalent size categories wild larvae appear to have daily rations substantially greater than those of cultured larvae. Other estimates of daily rations of striped bass larvae range widely. Miller (footnote 5) concluded that field-caught larvae (6.8 to 9.2 mm SL) consumed rations equivalent to 0.159 cal for rotifers or up to 2.958 cal for cladocerans. Doroshev (1970) estimated daily intake of laboratory-reared larvae to be 9.704 to 29.112 cal, consisting of *Cyclops* nauplii or small copepods. Our average calculated daily estimates for the different food concentrations for the 29-d experimental period fall within Miller's estimates of wild larvae (Table 8).

TABLE 8.—Mean daily caloric rations of striped bass larvae given five different food densities from D-7 to D-29.

Food density (*Artemia*/ml)	Mean overall daily caloric ration (calories/larva per d)
0.01	0.035
0.10	0.439
0.50	0.802
1.00	0.823
5.00	1.313

Energy Outputs

Our results suggest that there is compensatory growth in embryos and larvae that offsets initial egg size differences. The size ranges are not as broad in newly hatched larvae and larvae at first feeding (D-7) (seen in Table 5) as they are in the eggs. Likewise, initial egg size corresponds better to the size ranking of larvae at hatching age than it does to larvae at feeding age. The mean instantaneous growth coefficient during the 2-d embryonic period was 1.872 with a coefficient of variation (C.V.) of 8.5% (Table 5). From hatching to first feeding it was 0.647 with a decreased C.V. of 7.0%, an indication of narrowing diversity. Further compensatory growth was seen in tissue weights and standard lengths of feeding larvae (Figs. 4, 5), and convergence of sizes was seen in all food concentrations above 0.10 *Artemia*/ml. Weights were similar on D-25 and lengths on D-27. In the two higher food concentrations, sizes converged by D-17. Compensatory growth was documented years ago in salmon fry (Hayes and Armstrong 1942), so this is not necessarily unique to striped bass. Theilacker (in press) more recently found that growth rates of jack mackerel larvae varied with egg size.

Growth of feeding striped bass larvae was clearly tied to exogenous food consumption as seen in Figure 6. This relation is well established in other larval fishes (O'Connell and Raymond 1970; Saksena and Houde 1972; Laurence 1974; May 1974a; Houde 1977; Taniguchi in press).

Growth rates of our larvae, especially those in the higher food concentrations, are similar to findings with other populations of striped bass (Rogers et al. 1977). The most comparable study (Daniel 1976) included continuous introduction of *Artemia* for 10 d in concentrations of 0.004 to 0.030 nauplii/ml. Twenty-five days after hatching larvae grew to an average standard length of 8.5 mm. Fish used in the present study were longer than Daniel's in the two higher food concentrations and smaller in the three lower concentrations. As in our study, Daniel's larvae also grew directly in relation to food density. Tissue weights of Daniel's fish fed the 0.008 and greater *Artemia*/ml concentrations approximated those of our fish fed concentrations of 0.005 and above. Our larvae that fed at 5.0, however, were all heavier than Daniel's larvae. Lal et al. (1977) also cultured California striped bass larvae but in varying salinities. Larvae of comparable age feeding on *Artemia* (densities unreported) were similar to our larvae from the 0.50 nauplii/ml. Larvae from our higher densities were larger.

Oxygen consumption measurements varied directly with size, age, and temperature. Because temperature was held constant in all tests, age and size were the most influential factors affecting oxygen consumption, and these factors produced distinctive patterns. The high metabolic rates (Q_{O_2}'s) demonstrated by embryos and newly hatched larvae were probably the results of the activity accompanying hatching and of the high metabolic needs associated with rapid tissue growth and differentiation. These needs remained high into the period of feeding transformation and then leveled off to nearly constant rates after D-10. Similar patterns have been seen in other fishes (Smith 1957; Blaxter 1969). The relation of oxygen consumption to weight is usually described in a log-log transformation with a slope approximating 0.8 (Winberg 1956). Our slope of 0.72 shows that our equation describes the weight-metabolism relation up to the final size encountered. Laurence (1977) found winter flounder metabolism profoundly changed after metamorphosis resulting in a curvilinear pattern described best by a third degree polynomial equation. It is likely that striped bass would show similar tendencies when measured further along in development.

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[5] Miller, P. E., Jr. 1978. Food habit study of striped bass post yolk-sac larvae. The Johns Hopkins University, Chesapeake Bay Institute, Spec. Rep. 68, Ref. 78-8.

Reviews (Blaxter 1969; Eldridge et al. 1977) show that efficiencies during the strictly endogenous energy period of embryos and prefeeding larvae ranged from 40% to 70%. Our findings with striped bass tended toward the low side of this range. *Micropterus salmoides* was most similar to striped bass, with efficiencies of 35.2% to hatching and 43.9% to feeding (Laurence 1969). Like those of striped bass, the eggs of *M. salmoides* also possess large oil globules, and their larvae have similar predatory behavior. Gross growth efficiencies of aquatic consumers in general normally fluctuate between 15% and 35% (Welch 1968). Efficiencies of larval and postlarval fishes have also been found to be within this range (Ivlev 1939a; Laurence 1973, 1977). Ivlev (1945) believed postembryonic stages were restricted to efficiencies <35%, and fish normally have decreasing efficiencies with age (Parker and Larkin 1959; Theilacker footnote 4). All our efficiency values support these conclusions. Whether feeding or not, our older larvae had lower conversion efficiencies, probably resulting from increased metabolic demands associated with greater activity.

All organisms must balance input and output energies to successfully survive, grow, and ultimately reproduce. The essential relations between input and output energies and the equation which balances them have been well discussed by several authors (Winberg 1956; Warren and Davis 1967; Warren 1971; Wiegert 1976). This paper presents data that make up the basic parameters of an energy budget. The basic relation of these components can be presented in:

$$Q_I = Q_W + Q_G + Q_M$$

where Q_I = input energies, whether endogenous, exogenous, or a combination of the two
Q_W = waste energy
Q_G = growth energy
Q_M = metabolic energy.

All but Q_W have been studied by us, and the effects of food density and initial egg size have been discussed. In Figure 9 we present a graphic model of the energy budget of striped bass embryos and larvae fed the high ration diet (5.0 *Artemia*/ml). This model approximates that of Laurence (1977) except that we include input energies of yolk and oil, and we present the relations against time as rates (i.e., calories consumed or expended per 24 h period per organism).

When the energy budget is presented in these terms, some distinctive patterns emerge. Yolk provides a constant energy input until it is exhausted on or about D-7. Oil is used rapidly at first, then more slowly until yolk energy is no longer available and the animal initiates feeding. At this time, the larva increases its use of oil

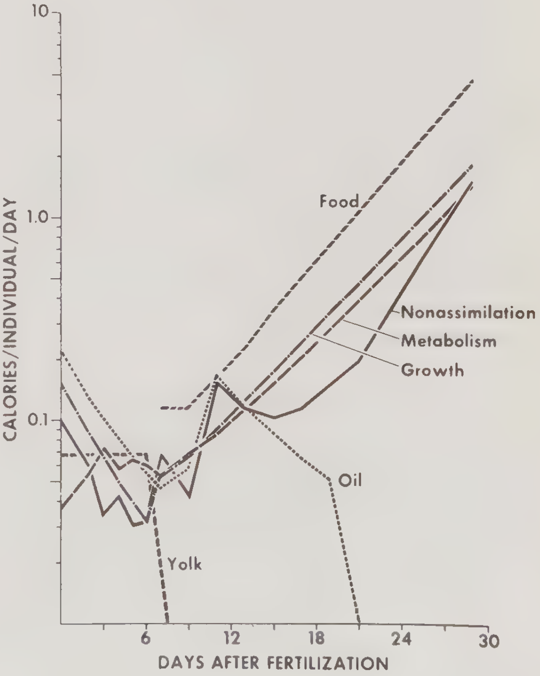

FIGURE 9.—Energy budget of input calories (yolk, oil, and food) and output calories (growth, metabolism, and nonassimilation) presented in calories per individual embryo or larva per day.

until exogenous feeding becomes established, after which it gradually decreases consumption of oil until oil energy is depleted. An initial adjustment to exogenous energy intake is followed by a continuously increasing exogenous input concomitant with decreased reliance on oil energy. Growth showed an interesting pattern that suggested it is closely linked to oil energy prior to feeding and to exogenous food energy after initiation of feeding. Growth rates declined steadily to D-6 and increased abruptly thereafter.

Metabolism increased steadily during incubation and hatching. After the energy consuming hatching process it decreased slightly to the onset of feeding. After D-7, increasing activity associated with feeding resulted in continuously increasing metabolism.

Nonassimilation is the energy remaining after metabolism and growth are subtracted from the total energy input. When energy input is endogenous, nonassimilation comprises poor utilization and/or redeposition of yolk and oil into other tissues. Nonassimilation of exogenous food is mostly due to undigested food. In this model nonassimilation fluctuated with oil input energy and growth to first feeding. It increased during adjustment to feeding and declined when both oil and food calories were available. As *Artemia* became the main energy source nonassimilation increased. Poor digestion in older larvae in the form of nearly intact *Artemia* in the intestines was seen commonly, especially in the high food rations.

The bioenergetics model and its parameters are presently being used to measure various abiotic and biotic stresses, including pollutants. It promises to be a useful method for assessing the effects of these factors.

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Metabolic Rate of the Albacore Tuna *Thunnus alalunga*

J. B. Graham[1] **and R. M. Laurs**[2]

[1] **Physiological Research Laboratory and Marine Biology Research Division, Scripps Institution of Oceanography; La Jolla, California 92093, USA**

[2] **National Marine Fisheries Services, Southwest Fisheries Center; La Jolla, California 92093, USA**

Abstract

The oxygen consumption rates ($\dot{V}O_2$) of 6 specimens (6 to 13 kg) of the albacore tuna *Thunnus alalunga* were measured at sea, using specimens collected 300 km west of San Diego, California (USA) during July and August, 1981. Fish were tested in a closed continuous-flow respirometer, where they swam at about 1.3 body lengths s^{-1} velocity in 15 ° to 19 °C water. The albacore tuna is a temperate pelagic species experiencing water temperatures from about 10 ° to 20 °C and attaining a maximum weight of 45 kg. The $\dot{V}O_2$ ranged from 1 249 to 3 336 ml h^{-1} (the mean $\dot{V}O_2$ for the 6 fish was 2 228 ml h^{-1}); such values approach those of mammals of a similar size and are 3 to 4 times those of most active fishes (e.g. sockeye salmon). Among fishes, the only higher $\dot{V}O_2$ values yet recorded were for the skipjack tuna *Katsuwonus pelamis*, a tropical species. The remarkably high metabolic rates of tunas are presumably correlated with their continuous swimming activity and the maintenance of endothermy. The exponent relating $\dot{V}O_2$ to body weight (1.18), although large, is not statistically different from the exponents for most other active vertebrates.

Introduction

Tunas, the most advanced and highly specialized group of fishes in the teleost family Scombridae, must swim continuously to maintain hydrostatic equilibrium (Magnuson, 1973, 1978) and to ventilate their gills (Roberts, 1978). Continuous swimming by tunas doubtlessly entails a large energetic investment (Gooding *et al.*, 1981; Stevens and Dizon, 1982). Moreover, the anatomical, physiological and biochemical specializations that are unique to tunas are all consistent with the hypothesis that these fish require high rates of oxygen consumption to sustain their body maintenance and locomotory costs (Gooding *et al.*, 1981; Stevens and Dizon, 1982; Graham *et al.*, unpublished observations). Verification of this hypothesis by direct measurement of the swimming metabolic rates of tunas is, however, technically difficult due to their generally large body size, fast swimming speeds, and poor survivorship in captivity.

Gooding *et al.* (1981) were the first to measure the swimming $\dot{V}O_2$ of tuna. They studied 0.4 to 6.0 kg specimens of skipjack tuna (*Katsuwonus pelamis*) swimming at speeds ranging from 50 to 75 cm s^{-1} in temperatures from 23 ° to 25 °C. The work by Gooding *et al.* revealed the following remarkable characteristics of skipjack tuna metabolism and swimming energetics: (1) skipjack tuna $\dot{V}O_2$ (0.522 mg O_2 g h^{-1}) was nearly the same as that of a mammal of similar size and thus much higher than that of most active fishes; (2) compared to a sockeye salmon (*Oncorhynchus nerka*, family Salmonidae) swimming at similar speeds but in 15 °C water, a skipjack tuna has a $\dot{V}O_2$ that is 2 to 5 times higher; (3) the rate of increase in $\dot{V}O_2$ with swimming velocity was proportionally less in skipjack tuna than in a sockeye salmon, implying that tunas, relative to salmonids, may be more efficient swimmers; (4) the $\dot{V}O_2$ of skipjack tuna was proportional to wet-body weight raised to a power of 1.19 (i.e. $\dot{V}O_2 \simeq W^{1.19}$), an exponent much higher than values (0.6 to 1.0) typical for active metabolism-body weight relationships in other vertebrates (Brett and Groves, 1979; Schmidt-Nielsen, 1979).

The notable results obtained for skipjack tunas by Gooding *et al.* (1981) invite additional experimentation with tuna swimming metabolism in order to verify these findings and understand how swimming energetics may vary among tuna species. Although their work was of extremely high quality, many of the $\dot{V}O_2$ determinations made by Gooding *et al.* were with groups rather than individual swimming skipjack tuna, and fish swimming speed could not be precisely controlled. Also, conclusions about the relative magnitude of the $\dot{V}O_2$ of skipjack tuna (and therefore all tuna species) relative to the $\dot{V}O_2$ of other active fishes (e.g. salmonids) may be biased somewhat by the

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water temperature differences (skipjack 23° to 25 °C, sockeye 15 °C) present in the existing comparative data.

The present paper reports investigations of the swimming $\dot{V}O_2$ of the North Pacific albacore tuna *Thunnus alalunga*, conducted on board the "David Starr Jordan", research vessel of the National Oceanic and Atmospheric Administration-National Marine Fisheries Service. Our objectives were to measure $\dot{V}O_2$ as soon as possible after capture. We have studied the albacore because it, unlike the skipjack tuna, is a temperate-zone species and thus would provide $\dot{V}O_2$ data directly comparable, in terms of habitat temperature, to that for sockeye salmon. Another objective of our work was to investigate the scaling of $\dot{V}O_2$ with body weight in *T. alalunga*. We also report some observations on the effects of temperature and hypoxia on the albacore. In addition to increasing our knowledge of the specializations of tunas for locomotion, investigations of tuna swimming physiology are important to an understanding of the migration and movements of these fishes and to ensure proper management of the fishery.

Materials and Methods

Specimens of *Thunnus alalunga* were caught by trolling feathered jigs in surface waters approximately 300 km west of San Diego, California (USA) in July and August, 1981. Sea surface temperatures in the area ranged from 17.5° to 19.0 °C. Hooked fish were brought on board within 60 s of striking a jig, and a hose with running seawater was immediately placed in the mouths to irrigate the gills during hook removal. Only fish without serious hook injury were selected for respirometer tests.

Swimming $\dot{V}O_2$ measurements were made on 6 albacore, ranging in weight from 6 to 13 kg. Each fish was initially submerged in a 200 liter tank containing chilled (15° to 17 °C), oxygenated seawater, and its gills were ventilated with flow from a submersible pump. After initial observations revealed the fish to be in good condition, it was transferred to the working section of a tunnel respirometer (Fig. 1), where continuously flowing water required it to swim in order to maintain a stationary position. A single-speed centrifugal pump (capacity 4 000 liters min^{-1}) circulated water from the reservoir (2 800 liters) through the working section of the respirometer and back to the reservoir. The parallel bypass channel and gate valve in the system (Fig. 1) permitted some modulation of flow through the working section. This was necessary initially to "train" fish to swim in the chamber (10 to 30 min) and to stimulate swimming throughout each experiment. A removable clear Lucite lid, fitted with a rubber gasket and held in place by wingnuts, was used to introduce or remove a fish from the respirometer. A black plastic cover over the front half of the lid darkened the chamber during experiments. This had a calming effect on the fish and, together with vertical black and white stripes painted inside the front part of the working section, may have provided orientation cues for maintaining station.

Refrigeration units in the reservoir maintained temperature between 14° and 18 °C. All pipes used in respirometer construction were PVC (15.2 cm i.d.). The 110 cm long aluminium working section (Fig. 1) was square in cross-section (26×26 cm), and tapered at each end (for 42 cm) to permit direct attachment to PVC flanges. A 23 cm long stack of 2 cm (i.d.) diam PVC collimator tubes in the anterior part of the working section helped to reduce turbulence. A small 45° grating was also installed anterior to the collimator (Fig. 1) to deflect water to the inner side of the working section and straighten flow from the upstream union with the bypass channel (Fig. 1). Dye injections were used to verify rectilinear flow through the working section.

A calibrated flow meter was used to determine water velocity in the working section. The average velocity was 0.73 m s^{-1}. Actual experimental velocities were higher, however, because of the solid blocking effects of fish body cross-sectional area (Webb, 1975). To take this into account, size-dependent velocity relationships had to be calculated as follows for each fish tested, using the methods described by Bell and Terhune (1970). Chamber velocity, U, is proportional to the product of the rated tunnel velocity, U_t, and the velocity factor speed increment, K, imposed by fish cross-sectional area,

$$U = U_t(1+K). \quad (1)$$

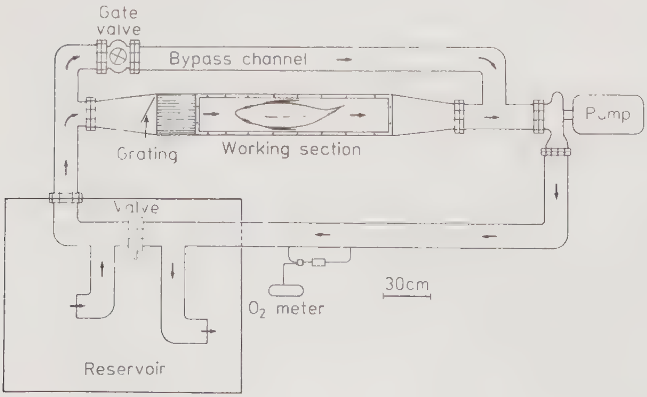

Fig. 1. Top view of albacore swimming respirometer. Arrows show direction of flow. Main return pipe is located at top of reservoir

K is estimated by

$$K = \tau \lambda \frac{A_0^{3/2}}{A_t}, \qquad (2)$$

where τ is 0.8, λ is 0.5 x (fish fork length ÷ body thickness), and A_0 and A_t are the cross-sectional areas of the fish and tunnel, respectively (Bell and Terhune, 1970).

The condition of albacore in the respirometer was continually monitored and tail-beat frequency was determined at regular intervals. Metabolic rate measurements were begun only after a fish had swum continuously for 1 to 2 h. Oxygen consumption rate ($\dot{V}O_2$) was estimated by monitoring the decline in respirometer O_2 level during 15 to 25 min intervals when the respirometer was closed and no water exchange occurred between it and the reservoir. The respirometer was closed by opening a gate valve between the intake and outflow pipes and capping the two reservoir ports (Fig. 1). The rate of O_2 decline (slope) when corrected for closed respirometer volume (342.5 liters), fish wet weight (volume), and background respiration, indicated fish $\dot{V}O_2$. Respirometer oxygen level was measured with a temperature-compensated Yellow Springs O_2 electrode (Model 54) in a housing which was circulated with water pumped from and back into the respirometer (Fig. 1). Before each test, the electrode was calibrated in air and water. Replicate $\dot{V}O_2$ measurements were made on all but one fish, and 20 to 30 min elapsed between each run. Because water temperature rose when the system was closed, runs had to be kept short and all albacore $\dot{V}O_2$ measurements were made under conditions where temperature increased by 2 or 3 C° during the run. The temperature-compensated probe permitted correction for the effects of heating on O_2 solubility, and tests with freshly killed fish were conducted to estimate background respiration.

All tests were carried out at water O_2 concentrations above 60% air saturation. In addition, observations were made on the behavioral responses to decreasing O_2 concentration to the point of suffocation for one fish. Also 3 inadvertent "tests" with fish at respirometer water temperatures of 11° to 12 °C provided additional information about the probable tolerance limits of albacore to low temperature.

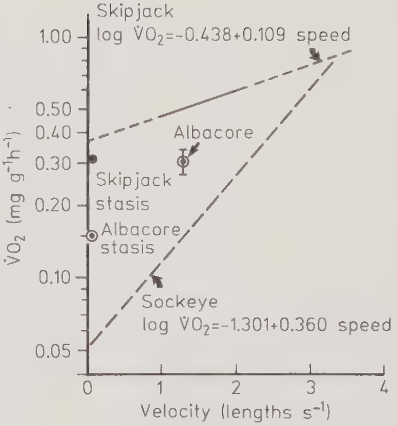

Fig. 2. Relationship between swimming speed and $\dot{V}O_2$ determined for 0.4 to 6.0 kg skipjack tuna (*Katsuwonus pelamis*) by Gooding *et al.* (1981) and the weighted mean $\dot{V}O_2$ (mg g^{-1} h^{-1} ±95% confidence intervals) determined for 6 to 13 kg albacore (*Thunnus alalunga*) swimming at 1.3 lengths s^{-1} in present study. Stasis $\dot{V}O_2$ estimates for albacore (Brill, personal communication) and skipjack tuna (Brill, 1979) are included for comparison, as is the $\dot{V}O_2$-velocity relationship of sockeye salmon (*Oncorhynchus nerka*) at 15 °C (Brett and Glass, 1973; Gooding *et al.*, 1981). Albacore data were obtained at 15° to 19 °C, skipjack at 23° to 25 °C

Results and Discussion

Table 1 summarizes *Thunnus alalunga* body-size information, corrected respirometer swimming speeds (Eqs. 1 and 2), mean tail beat frequencies, and the $\dot{V}O_2$ estimates obtained for the 6 albacore in this study. The mean combined $\dot{V}O_2$ for all fish is 2 228 ml h^{-1} $fish^{-1}$. Expressed in terms of unit body weight, mean $\dot{V}O_2$ is 0.212 ml g^{-1} h^{-1} (=0.303 mg g^{-1} h^{-1}, Fig. 2). Calculated swimming speeds vary directly with size and range from 93 to 115 cm s^{-1}, and there is no correlation between $\dot{V}O_2$ and swimming speed (Table 1). Each albacore maintained a steady tail-beat frequency during the test period, and the range of rates observed (2.13 to 2.36 Hz) for all fish is similar to values reported for other scombrids swimming at 1.3 lengths

Table 1. *Thunnus alalunga*. Body size, swimming speed and respiration data at 15° to 19 °C. $\dot{V}O_2$ data are weighted means

Fish No.	Weight (g)	Fork length (cm)	Swimming velocity (cm s^{-1})	Swimming velocity (lengths s^{-1})	Tail-beat frequency Hz±(95%)	Mean $\dot{V}O_2$ (ml g^{-1} h^{-1})	SD	N	Mean total O_2 consumption (ml h^{-1})	Minimum speed[a] (lengths s^{-1})
1	6 245	67.6	92.6	1.37	2.31 (0.20)	0.200	0.049	3	1 249	0.72
2	9 740	79.5	104.9	1.32	2.14 (0.07)	0.159	0.044	4	1 553	0.57
3	11 810	83.7	109.6	1.31	2.24 (0.04)	0.175	0.003	4	2 070	0.51
4	13 600	87.5	114.6	1.31	2.23 (0.05)	0.245	0.020	4	3 336	0.47
5	9 170	77.0	101.6	1.32	2.13 (0.10)	0.179	–	1	1 643	0.62
6	9 890	82.0	108.2	1.32	2.36 (0.07)	0.286	0.020	4	2 831	0.54
$\bar{X}$	10 076	79.6	105.3	1.33	2.24	0.212[b]			2 227.5	

[a] Estimated from Dotson (1976): $V_{\min} = \frac{l_f}{D_e/2(A)}$, where A is body lifting area, l_f is lift required for hydrostatic equilibrium, D_e is sea-water density (see Magnuson, 1973)

[b] 0.212 ml O_2 g^{-1} h^{-1} = 0.303 mg O_2 g^{-1} h^{-1}

s^{-1} (Fig. 16 in Magnuson, 1978). Stride length coefficients (i.e., the number of body lengths moved per tail beat) of the albacore in Table 1 range from 0.56 to 0.62, which is within the range of values found for other scombrids (Magnuson, 1978; Brill and Dizon, 1979). The variation in tail-beat frequency observed among different fish was not correlated with either body size or corrected swimming velocity.

The swimming velocities of albacore tuna in these tests ($\bar{x}$ 1.3 lengths s^{-1}) were similar to the mean speeds of the skipjack tuna *Katsuwonus pelamis* tested by Gooding *et al.* (1981; range 0.9 to 2.0 lengths s^{-1}). Table 1 also indicates the minimum swimming speed estimates for each fish based on the relationship determined for albacore tuna by Dotson (1976). Minimum speed is defined as the slowest speed a negatively buoyant fish (such as all tuna) could swim and still maintain hydrostatic equilibrium (Dotson, 1976). Minimum speed varies among species, and depends primarily upon morphological features such as the presence or absence of a gas bladder, pectoral fin size (area) and body shape (Magnuson, 1978). It is apparent that the velocity of each fish in the respirometer was faster than its minimum speed requirement by a mean factor of 2.4.

Fig. 2 compares the mean weight-specific $\dot{V}O_2$ (0.303 mg O_2 g^{-1} h^{-1}) of the 6 albacore tuna swimming at a mean speed of 1.3 lengths s^{-1} with the $\dot{V}O_2$-velocity linear regression for skipjack tuna (Gooding *et al.*, 1981). Also shown in Fig. 2 is the "stasis" $\dot{V}O_2$ for a 1.96 kg skipjack tuna (the mean weight of fish tested by Gooding *et al.*) calculated from the $\dot{V}O_2$-weight regression determined by Brill (1979) for sedated spinalectomized fish. (Stasis $\dot{V}O_2$ is determined from measurements on sedated immobilized fish in order to provide an estimate of maintenance metabolic activities that are otherwise masked by swimming metabolism.) Brill (personal communication) also allowed us to include his unpublished stasis $\dot{V}O_2$ measurements for two albacore (3.3 and 3.5 kg) in Fig. 2. Finally, and for additional comparison, the $\dot{V}O_2$-velocity regression for a 1.8 kg sockeye salmon (*Oncorhynchus nerka*) at 15 °C is included (as shown in Gooding *et al.*,1981; data from Brett and Glass, 1973).

Fig. 2 shows the lower rate of increase in $\dot{V}O_2$ with velocity found for skipjack tuna (Gooding *et al.* 1981) relative to sockeye salmon. At low speed, skipjack tuna at 23 ° to 25 °C clearly have higher maintenance costs than do sockeye salmon at 15 °C; however, the energetic cost of swimming faster is proportionately less in skipjack tuna, possibly because of their streamlined body and improved mechanical efficiency (Gooding *et al.*,1981; Stevens and Dizon, 1982). Although there are no $\dot{V}O_2$ data for skipjack tuna swimming slower than 0.9 lengths s^{-1}, extrapolation of the Gooding *et al.* $\dot{V}O_2$-velocity line to zero velocity gives a "resting" $\dot{V}O_2$ estimate of 0.365 mg g^{-1} h^{-1}, which is 1.2 times greater than Brill's stasis $\dot{V}O_2$ estimate for a 1.96 kg fish (0.307 mg g^{-1} h^{-1}). Assuming that the $\dot{V}O_2$ velocity relationship of albacore parallels that of skipjack tuna, one can extrapolate to zero velocity to obtain a "resting" $\dot{V}O_2$ of about 0.224 for albacore (Fig. 2), which is 1.5 times above the stasis rate determined for this species by Brill (personal communication), and only slightly more than the ratio between resting and stasis $\dot{V}O_2$ in skipjack tuna. The overall similarity between these ratios in both *Thunnus alalunga* and *Katsuwonus pelamis* suggests that these species incur comparable increases in metabolic cost during swimming.

Fig. 2 additionally shows that at 1.3 lengths s^{-1} swimming speed, albacore weight-specific $\dot{V}O_2$ is twice the rate of sockeye salmon and 60% of that of skipjack tuna. Thus, even though albacore typically occur in cooler waters than do tropical skipjack tuna (Laurs and Lynn, 1977), their metabolic rate at 15 ° to 19 °C is nearly as high as that of a skipjack tuna at 23 ° to 25 °C. Also, the maintenance by the albacore of a metabolic rate twice that of a sockeye salmon at 15 °C suggests that an elevated metabolic rate is typical of all tuna species.

The following factors may explain the differences between albacore and skipjack tuna $\dot{V}O_2$. Both these species are endothermic (Graham and Dickson, 1981). Skipjack tuna tested at 23 ° to 25 °C would be expected to have a core body temperature of about 26 °C (Dizon and Brill, 1979), which is slightly warmer than deep core and red muscle temperatures expected to prevail in an albacore (21 ° to 25 °C) in 17 ° to 18 °C water (Graham and Dickson, 1981). Because it is warmer, the skipjack tuna may use more O_2 (Stevens and Dizon, 1982) and thus have a higher $\dot{V}O_2$ at a given speed and water temperature. Albacore have lower amounts of aerobically active red muscle than skipjack, 4.1% of body mass vs 7.3%, respectively (Graham *et al.*, unpublished observations). Based on published values for red muscle $\dot{V}O_2$ (Stevens and Neill, 1978), we calculate that this difference in red muscle accounts for 20% of the $\dot{V}O_2$ difference. However, relative activity differences between albacore and skipjack tuna in the two swimming experiments do not correlate with $\dot{V}O_2$ differences. Although swimming velocities were similar in tests with albacore and skipjack tuna (see above), albacore swam 2.4 times faster than their minimum speed for hydrostatic equilibrium (Table 1) while skipjack tuna tested by Gooding *et al.* (1981) swam at only 85% of their minimum speed. Gooding *et al.* attributed differences in the observed and expected speeds of skipjack tuna in their experiments to condition factors (e.g. reductions in body fat and thus density and average gut fullness) that occur in captivity as a result of feeding schedule, nutrition, and exercise.

Body size also has an effect on the $\dot{V}O_2$ differences seen between the albacore and skipjack tunas. Fig. 3 compares total $\dot{V}O_2$ (ml O_2 h^{-1}) vs body weight for both species. The equation for albacore is

$$\log \dot{V}O_2 = 1.395 + 1.18 \log W, \qquad (3)$$

where W is weight in g. The correlation between $\dot{V}O_2$ and weight is significant ($r=0.81$, $N=20$, $p= <0.05$; 95% confidence intervals for the slope value are ± 0.53). The line for skipjack tuna was taken from an equation relating $\dot{V}O_2$,

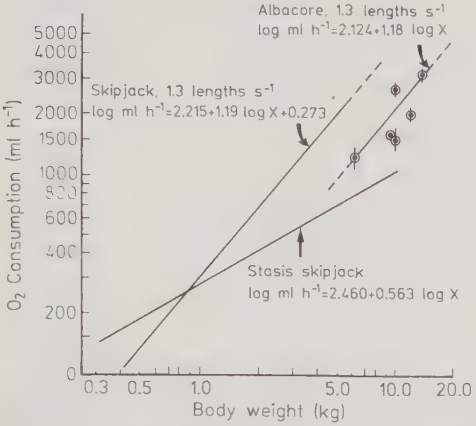

Fig. 3. *Thunnus alalunga* and *Katsuwonus pelamis.* Relationships between total O_2 consumption (ml h^{-1}) and body weight in albacore and skipjack tuna swimming at 1.3 lengths s^{-1} and the change in skipjack stasis $\dot{V}O_2$ with body weight (Brill, 1979). Vertical lines through points for albacore are standard errors of the mean $\dot{V}O_2$ estimate for each fish

weight, and speed (Gooding *et al.*, 1981),

$$\log \dot{V}O_2 = 1.20 + 0.19 \log W + 0.21\, S, \qquad (4)$$

where $\dot{V}O_2$ is in mg g^{-1} h^{-1}, W is weight (g) and S is speed (lengths s^{-1}). Corrections were applied to convert mg O_2 g^{-1} h^{-1} to ml O_2 h^{-1}, and to enable direct comparison with albacore, the equation was evaluated at $S = 1.3$ lengths s^{-1}. This resulted in a slope of 1.19 and a speed constant of 0.273 (Fig. 3). Also shown in Fig. 3 is the stasis $\dot{V}O_2$-body weight relationship for skipjack (Brill, 1979):

$$\log \dot{V}O_2 = 0.93 + 0.56 \log W, \qquad (5)$$

where $\dot{V}O_2$ is in mg h^{-1} (converted to ml h^{-1} for comparison) and W is in g.

Fig. 3 reveals the striking similarity between the slopes of the $\dot{V}O_2$-body weight regression equations for albacore (1.18) and skipjack tuna (1.19). The $\dot{V}O_2$-size slope values determined for most vertebrates generally increase with activity, and approach and sometimes exceed 1.0 (Brett and Groves, 1979; Schmidt-Nielsen, 1979). Thus, the values for both tuna species are unusually high. It is noteworthy that independent studies with two different tuna species (Gooding *et al.*, 1981, with skipjack and the present work with albacore) both arrived at atypically high and very similar values for the $\dot{V}O_2$-weight exponent. However, in the case of the albacore, the 95% confidence intervals for the slope extend this value from 0.65 to 1.71. Thus, no significant difference is seen in the weight exponent for total active metabolism in the albacore and typical values for other active vertebrates (Brett and Groves, 1979; Schmidt-Nielsen, 1979). Gooding *et al.* (1981) did not indicate slope confidence intervals for their 1.19 weight exponent. This value was obtained from a multiple regression analysis (Eq. 4) in which the effects of both weight and speed on $\dot{V}O_2$ were evaluated. Size and speed are clearly interdependent in tunas (Magnuson, 1973, 1978), and Gooding *et al.* (1981) calculated a weight exponent probably biased by this analytical technique. This is shown by the lack of agreement in the data of Brill (1979) and Gooding *et al.* (1981) (present Fig. 3) where, at body weights smaller than 0.9 kg, the stasis $\dot{V}O_2$ of skipjack, as predicted by Eq. (5) actually exceeds predicted $\dot{V}O_2$ at 1.3 s^{-1} (from Eq. 4). When Gooding *et al.* (1981, their Fig. 3) applied a speed correction factor to their data, they found skipjack total metabolism (i.e., mg O_2 h^{-1}) to vary with a mass exponent of about 1 (zero if $\dot{V}O_2$ is computed as mg O_2 g^{-1} h^{-1}). We have estimated the confidence intervals to be about ±0.3 for data presented in Fig. 3 of Gooding *et al.* (1981). While this exponent (1 ± 0.3) remains beyond the stasis $\dot{V}O_2$-mass exponent of Brill (0.56 ± 0.07), it is not excessively large or unexpected for an active fish. Thus, present evidence does not unequivocally support the conclusion that an unusually large metabolism-weight exponent is present in tunas. Gooding *et al.* (1981), however, did additionally cite several independent lines of evidence (e.g. the scaling of heat production and red muscle metabolism in skipjacks) to support their conclusion that the 1.19 weight exponent is valid. Further experimentation is thus required to discern fully the consequences of size and activity on the metabolism of tunas.

Additional results obtained for albacore tuna in the respirometer suggest that adverse effects result from prolonged exposure to low temperature and also permit some preliminary conclusions about the effects of low ambient O_2 levels. Graham and Dickson (1981) showed that under the experimental conditions of their study, the albacore tuna is unable to regulate red muscle temperature for long periods below 12 °C. In the present study, 3 fish placed in the respirometer with initial water temperatures of from 11° to 12 °C lost equilibrium within 1 to 2 h. Since fish in these tests were in the same size range as those used by Graham and Dickson, size was not a factor and no other experimental procedures were implicated in the failure of these test fish. All 3 fish initially swam vigorously; however, within the confines of the respirometer they may not have been able to increase activity sufficiently to prevent hypothermia. Albacore swimming in nature spend from 10 to 90% of their time in 9° to 12 °C water (Laurs *et al.*, 1980). Unstressed free-swimming fish may be better able to control heat balance as well as alternate periods in cool and warm water (Graham and Dickson, 1981).

Fish No. 6 (Table 1) was kept in the sealed respirometer until it suffocated. Owing to changes in water temperature while the system was closed, we were unable to discriminate between the effects of elevated temperature and hypoxia on the lethal limit of this fish which occurred at about 37% of air saturation (57 mm Hg O_2 partial pressure) and at 22 °C. The first effects of hypoxia were noted at about 58% saturation (90 mm Hg) in 18° to 19 °C water when the fish increased its mouth gape and made occasionally larger tail thrusts. Between 55 and 45% saturation (85 to 70 mm Hg), intermittent opercular pumping was noted and caudal frequency sporadically increased. Since these responses occurred at temperatures within the range typically encountered by albacore (Laurs and Lynn, 1977) behavioral aviodance responses to hypoxia might normally be initiated by this O_2 level in the natural environment. Gooding *et al.* (1981) found that skipjacks exhibited behavioral responses to hypoxia beginning at about 90 mm Hg (23 ° to 24 °C), and that about 4 h exposure to this level of hypoxia proved fatal. By contrast, Dizon (1977) determined that the yellowfin tuna (*Thunnus albacares*) is much more tolerant of low O_2 than is the skipjack tuna (*Katsuwonis pelamis*) which may be related to the frequent occurrence of yellowfin tuna in or near O_2 minimum zones.

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DISTRIBUTION OF ICHTHYOPLANKTON IN THE SOUTHERN CALIFORNIA BIGHT

DENNIS GRUBER
Institute of Marine Resources, A-018
University of California, San Diego
La Jolla, California 92093

ELBERT H. AHLSTROM
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

MICHAEL M. MULLIN
Institute of Marine Resources, A-018
University of California, San Diego
La Jolla, California 92093
(Address correspondence to this author.)

ABSTRACT

Larval fish were sampled by oblique 1-meter net and neuston net tows in the Southern California Bight quarterly from 1974 through 1976. The northern anchovy, *Engraulis mordax,* was much more abundant in both types of collections than were all other kinds of larvae combined, but some other fairly common species were found in only one type of tow. Subjective evaluation and analysis of recurrent groups established larval groupings that were distinguished primarily by nearshore versus offshore distribution and summer-fall versus winter-spring occurrence.

RESUMEN

Larvas de peces muestreadas trimestralmente entre 1974 y 1976 en arrastres oblicuos de redes neuston y de 1 metro en la Bahía del Sur de California. En ambos tipos de recoleciones, la anchoveta *Engraulis mordax* era mucho más abundante que todas las otras clases de larvas combinadas, pero otras especies bastante comunes fueron encontradas en sólo un tipo de arrastre. A través de la evaluación subjetiva y el análisis de groups recurrentes se establecieron agrupaciones de larvas que se distinguieron principalmente por su distribución, cerca de la costa o mar afuera, y aperecer durante los periodos de verano-otoño o en invierno-primavera.

INTRODUCTION

In studies of ichthyoplankton off California over the last three decades, the California Cooperative Oceanic Fisheries Investigation (CalCOFI) has emphasized the sampling of eggs and larvae of California Current pelagic species such as the sardine, which declined dramatically in the late 1940s. Recently, importance of recreational fisheries and increased human modification of California's nearshore zone have prompted concern for the fish populations residing there.

The distributions and abundances of some demersal species with pelagic eggs and larvae have been studied in samples from the CalCOFI surveys (Ahlstrom 1965), and many groups of inshore fishes are represented as larvae in CalCOFI collections, but the early surveys did not adequately sample areas close to shore. Depth increases rapidly with distance from shore off southern California, and the spawning of some neritic species is presumably restricted to a narrow band along the coastline and around the channel islands, banks, and seamounts. Pelagic larvae of such species are subject to dispersal by currents and must somehow remain in or return to the coastal zone in sufficient numbers to maintain adult populations (cf. Leis and Miller 1976 for larvae in Hawaiian waters). The larvae of some inshore spawners may develop rapidly enough to maintain their position in the nearshore zone, even though affected by longshore currents; such species would not be well represented in offshore surveys. Many larvae of species with longer larval life must be carried offshore by currents, especially by Ekman drift during periods of upwelling. Shoreward transport of such larvae by subsurface currents generated during upwelling is also possible (Peterson, Miller, and Hutchinson 1979).

The Southern California Bight lies inshore of the southward-flowing California Current. The bight's surface circulation is generally a cyclonic gyre; nearshore currents alternate between flowing south-southwest or north-northwest, though the latter flow dominates (Tsuchiya 1980). This study was carried out to refine the knowledge of seasonal and areal distributions of pelagic larval fish within the Southern California Bight, emphasizing the nearshore zone not sampled by CalCOFI.

METHODS

Southern California Bight Study (SCBS) station positions were chosen to represent quasi-logarithmic distances from the mainland shore (Table 1); SCBS lines 300, 200, and 100 correspond to CalCOFI lines 87, 90, and 93, respectively (for a map, see Eppley et al. 1977, or Eppley, Sapienza, and Renger 1978). SCBS cruises 1 through 9 cover more than two years—from September 1974 through January 1977.

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TABLE 1

Depths and Locations of Stations Sampled for Ichthyoplankton in the Southern California Bight Study (SCBS), 1974–77

Station number	Depth (m)	Distance offshore (km)	Position	
301	16	0.9	33°54.3′N	118°25.5′W
302	18	1.9	33°55.1′N	118°27.2′W
303	42	5.6	33°53.8′N	118°28.8′W
304	320	19	33°50.4′N	118°36.2′W
305	920	46	33°45.5′N	118°47.6′W
306	1650	98	33°30.1′N	119°20.0′W
201	36	0.9	33°29.4′N	117°44.9′W
202	54	1.9	33°29.0′N	117°45.5′W
203	90*	5.6	33°28.0′N	117°47.5′W
205	730	52	33°17.3′N	118°10.4′W
206	1240	96	33°07.0′N	118°31.3′W
San Onofre	5	0.5	33°20.1′N	117°30.4′W
101	20	0.9	32°57.4′N	117°16.5′W
102	38	1.9	32°57.3′N	117°17.3′W
103	230*	5.6	32°56.8′N	117°18.9′W
105	1000	41	32°52.2′N	117°37.8′W
106	1850	107	32°31.6′N	118°07.0′W

*Station position and depths of #103 and 203 varied.

Stations were sampled quarterly with the exception of December 1974, when no cruise was undertaken.

Ichthyoplankton was collected with oblique plankton net hauls and surface or neuston net hauls made simultaneously at each station, except at some very shallow stations where only the neuston net was used. Oblique hauls were made with the standard CalCOFI-type net constructed of 505-μm nylon netting with a mouth diameter of one meter and a straining surface-(pore area)-to-mouth-area ratio of approximately five to one. A digital flow meter was centered in the circular mouth opening, attached to the tubular metal frame.

Oblique samples were collected, preserved, and processed following CalCOFI guidelines as described by Kramer et al. (1972). During cruise SCBS 4, the maximum amount of towing wire let out was reduced from 300 to 200 m. In shallow water on all cruises, the depth of tow was adjusted to avoid hitting the bottom.

The neuston frame carried an identical net to that used for oblique hauls, but the mouth of the net was modified from a circle to a rectangle, and for buoyancy, styrofoam floats were placed inside the frame ends (Ahlstrom and Stevens 1976). No flow meter was attached; the neuston net was towed for a minimum of 10 minutes. Neuston collections were preserved and processed similarly to the oblique collections.

All net tows were done during daylight hours, leading to two potential sources of bias. The abundances of those juveniles and late larval stages that are able to see and avoid the net are underestimated. Also, a few species (e.g., *Tarletonbeania crenularis*) would be caught in greater numbers in night hauls because they migrate to the surface waters then.

Most samples were completely sorted for all fish eggs and larvae; for stations 303, 305, 306, 205, and 105 on cruise SCBS-2, only 25 percent of the anchovy larvae were removed and counted, but all other fish larvae were removed from these samples.

Identification of larvae was to species level when possible, but taxonomic difficulties exist in several important groups. The most notable is the rockfish genus *Sebastes,* which includes 48 species known to spawn in the Southern California Bight (Miller and Lea 1972). The genera *Citharichthys* (sand dabs), *Hypsoblennius* (blennies), and *Paralabrax* (basses) each include three local species.

We directly compared the distributional records of different taxa to obtain subjective patterns, at least for the relatively common species. Because the number of samples was fairly large, we also applied a statistical grouping technique—the analysis of recurrent groups—that has previously been applied to communities of adult fish (e.g. Fager and Longhurst 1968), benthos (e.g. Lie and Kelley 1970), and zooplankton (e.g. Fager and McGowan 1963). We chose this approach because of the infrequent occurrence of most species (Table 2), and analyzed data from oblique and neuston tows separately. We tested several levels of affinity at which to form groups, since the level of affinity determines how two species can differ in frequency of occurrence and still be placed in the same group. We also analyzed both the entire set of data and the subset of species occurring at least 5 times; this had relatively little effect on major groupings, though analysis of the complete set resulted in some groups of rare species that were not found in the subset analysis.

The species in the resulting groups are frequent components of each other's biotic environments (or, in the extreme case, the very common species in a group are usual components of the environment of the group's very rare species), both seasonally and geographically, though our method of sampling precludes detecting differences in vertical distributions of species in the same group (see below). Although the members of a group necessarily have similar patterns of occurrence, they need not have similar patterns of abundance. The latter relation was tested for the major groups defined from oblique hauls by calculating a coefficient of rank correlation (Tate and Clelland 1957) between the abundances of species in each possible pairing for those samples in which the entire group occurred, and establishing a matrix of correlation coefficients for all pairs within the group.

TABLE 2

Taxa That Occurred in at Least 5 Oblique or Neuston Tows in the Southern California Bight, Ranked in Order of Decreasing Numerical Abundance in Oblique Tows

	Zone	Spawning type	Mean larvae/10 m^2	% of total larvae for oblique hauls	Mean larvae/10 m^2 in positive hauls	No. of occurrences	% of occurrences in 112 oblique hauls	Rank by occurrence in oblique hauls	% of occurrences in 127 neuston hauls
1. *Engraulis mordax*	C	P	733.2	82.83	774.8	106	94.6	1.0	57.4
2. *Sebastes* spp.	C	O	36.5	4.12	52.4	78	69.6	2.0	19.7
3. *Leuroglossus stilbius*	O	P	33.0	3.72	82.0	45	40.2	5.0	
4. *Stenobrachius leucopsarus*	O	P	19.5	2.20	42.0	52	46.4	4.0	
5. *Genyonemus lineatus*	C	P	15.0	1.70	44.3	38	33.9	7.0	14.2
6. *Merluccius productus*	O	P	14.4	1.63	59.7	27	24.1	12.0	
7. *Citharichthys* spp.	C	P	5.0	0.68	22.0	60	53.5	3.0	3.9
8. *Bathylagus ochotensis*	O	P	3.9	0.44	15.6	28	25.0	10.0	
9. *Paralichthys californicus*	I	P	3.0	0.34	8.6	39	34.8	6.0	
10. *Hypsoblennius* spp.	I	D	2.2	0.25	12.8	19	17.0	15.5	18.1
11. *Pleuronichthys verticalis*	I	P	2.1	0.24	8.4	28	25.0	10.0	
12. *Seriphus politus*	I	P	1.9	0.22	12.0	18	16.1	17.5	5.5
13. *Paralabrax* spp.	I	P	1.8	0.20	7.7	26	23.2	13.0	
14. *Peprilus simillimus*	C	P	1.6	0.18	9.7	18	16.1	17.5	
15. *Triphoturus mexicanus*	O	P	1.3	0.15	6.3	23	20.5	14.0	
16. Gobiidae	C	D	1.2	0.14	4.8	29	25.9	8.0	
17. *Argyropelecus* spp.	O	P	1.1	0.12	4.4	28	25.0	10.0	
18. *Sardinops caeruleus*	C	P	1.0	0.11	15.6	7	6.3	29.0	
19. *Pleuronichthys ritteri*	I	P	0.5	0.06	9.8	6	5.4	32.0	
20. *Parophrys vetulus*	I	P	0.5	0.05	5.4	10	8.9	24.0	
21. *Hypsopsetta guttulata*	I	P	0.5	0.05	4.8	11	9.8	22.0	
22. *Tarletonbeania crenularis*	O	P	0.5	0.06	3.2	19	17.0	15.5	
23. *Argentina sialis*	O	P	0.4	0.05	9.2	5	4.5	36.5	
24. *Oxyjulis californica*	I	P	0.4	0.05	4.9	10	8.9	24.0	
25. *Trachurus symmetricus*	O	P	0.4	0.05	4.2	12	10.7	20.5	6.3
26. *Lampanyctus* spp.	O	P	0.4	0.05	2.8	16	14.3	19.0	
27. *Lyopsetta exilis*	C	P	0.3	0.04	7.2	5	4.5	36.5	
28. *Bathylagus pacificus*	O	P	0.3	0.04	5.3	7	6.3	29.0	
29. Blennioidei	C	D	0.3	0.03	4.2	7	6.3	29.0	
30. *Hippoglossina stomata*	I	P	0.3	0.03	3.8	8	7.1	26.5	
31. *Danaphos oculatus*	O	P	0.3	0.03	3.6	8	7.1	26.5	
32. *Protomyctophom crockeri*	O	P	0.3	0.03	2.7	12	10.7	20.5	
33. *Diogenichthys laternatus*	O	P	0.2	0.03	5.5	5	4.5	36.5	
34. *Bathylagus wesethi*	O	P	0.2	0.02	4.0	6	5.4	32.0	
35. *Stomias atriventer*	O	P	0.2	0.02	3.5	5	4.5	36.5	
36. Clinidae	I	D	0.2	0.02	2.5	10	8.9	24.0	
37. *Tetragonurus cuvieri*	O	P	0.1	0.01	2.8	5	4.5	36.5	
38. *Diaphus theta*	O	P	0.1	0.01	2.0	5	4.5	36.5	
39. *Chromis punctipinnis*	C	D	0.1	0.01	1.9	6	5.4	32.0	
Atherinidae	I	S							24.4
Cololabis saira	C	S							22.8
Exocotidae	C	S							5.5
Medialuna californiensis	C	P							4.7
Girella nigricans	I	P							4.7
Scorpaenichthys marmoratus	C	D							3.9
Hexagrammos decagrammus	C	D							3.9

In cases of ties, the taxon with the greatest abundance in those samples in which it occurred (positive hauls) is ranked first. Unranked taxa occurred at least 5 times only in neuston tows. For ''zone'', I is inshore, O is offshore, C is inshore and offshore. For ''spawning type'', P is pelagic oviparous, D is demersal oviparous, O is ovoviviparous, S is a special case. S for Atherinidae indicates demersal in beach sand or floating attached egg mass; S for *Cololabis* and Exocoetidae indicates floating attached egg mass.

RESULTS

Abundances of Taxonomic Categories

Thirty-nine families of larval fish were found in oblique and neuston collections; of these, Engraulidae, Scorpaenidae, Bathylagidae, Myctophidae, Sciaenidae, Bothidae, Merlucciidae, and Pleuronectidae were responsible for over 98 percent of all larvae enumerated in the oblique hauls.

The abundances and/or frequencies of all taxa of larvae that occurred in at least five oblique or five neuston hauls are given in Table 2.

The northern anchovy, *Engraulis mordax,* (the only engraulid sampled) occurred in 95 percent of all oblique hauls (Table 2) and accounted for 83 percent of all larvae enumerated. It also was the most frequent (73 occurrences in 127 hauls) in neuston tows, where anchovy eggs were 15 times more abundant than all other fish eggs.

As expected, the neuston tows gave a somewhat different picture of the relative importance of taxa, though comparisons of absolute abundances are not possible since the volume filtered was not measured. Only 34 kinds of larvae were caught compared to 71 kinds in oblique tows. Atherinids (predominantly the grunion *Leuresthes tenuis*) occurred only twice in oblique tows but were found in almost 25 percent of the neuston tows and were particularly abundant in June 1975 at the shallowest station (San Onofre). The saury, *Cololabis saira,* occurred in 23 percent of the neuston tows and not at all in the oblique tows. The other groups occurring in over 10 percent of the neuston tows were *Genyonemus lineatus* (white croaker), *Sebastes* spp., and *Hypsoblennius* spp., all of which were also frequent in oblique tows. Flying fish (Exocoetidae) and *Hexagrammos decagrammus* (kelp greenling) were never taken in oblique tows, but occurred 7 and 5 times, respectively, in neuston tows.

Conversely, several types of larvae encountered frequently in the oblique tows were found in fewer than 5 neuston tows (*Leuroglossus stilbius, Stenobrachius leucopsarus, Merluccius productus, Paralichthys californicus, Pleuronichthys verticalis, Paralabrax* spp., *Peprilus simillimus, Bathylagus ochotensis, Triphoturus mexicanus, Argyropelecus* spp., and Gobiidae).

Geographical and Seasonal Patterns of Taxa and of Recurrent Groups

General zones of occurrence for larvae, based on cumulative records from both CalCOFI and SCBS cruises, are included in Table 2; Table 3 shows seasonal and inshore/offshore distributional patterns for some important larvae on SCBS cruises. Stations were arbitrarily categorized (see Table 3) with regard to depth and distance from the mainland as "nearshore," "intermediate," or "offshore."

Several kinds of larvae, especially from taxa whose adults are mesopelagic, were found primarily at offshore stations (Table 3A). Larvae of *Leuroglossus stilbius, Bathylagus ochotensis, Argyropelecus* spp. (hatchetfish), and *Merluccius productus* (Pacific hake) occur in greatest abundance below the upper mixed layer (Ahlstrom 1959), and adults of the myctophids *Stenobrachius leucopsarus, Triphoturus mexicanus, Protomyctophum crockeri,* and *Tarletonbeania crenularis* are known to inhabit fairly deep water. Larvae of *Trachurus symmetricus* (jack mackerel) are known to be most abundant in offshore waters (Ahlstrom and Ball 1954; Ahlstrom 1969). Most of the larvae in Table 3A were rarely taken in the inshore zone (except *S. leucopsarus),* but most were well represented in the intermediate zone, and *S. leucopsarus* was most abundant there.

Some larval taxa occurred primarily inshore, though most were also represented in the intermediate zone (Table 3B). The bothid flatfish *Paralichthys californicus* (California halibut) and the pleuronectid flatfish *Pleuronichthys verticalis* (hornyhead turbot) occurred at very few offshore stations, and both early and late larval stages were collected at inshore stations. CalCOFI data from 1955 through 1960 also establish these larvae as being most abundant inshore (Ahlstrom and Moser 1975). Adults of *Hypsoblennius* spp. are restricted to shallow water and spawn demersal eggs, and greatest abundances of larvae on SCBS cruises were in the inshore and intermediate zones. The sardine *Sardinops caeruleus* is included in the inshore group even though earlier CalCOFI data show it occurring both inshore and offshore (Ahlstrom 1959a). Based on the neuston tows, the Atherinidae (grunion) also belong to the inshore group.

Cosmopolitan taxa occurred regularly in all three zones (Table 3C), as did the anchovy (below). *Sebastes* spp. and the bothid flatfishes *Citharichthys* spp. generally exhibited higher concentrations of larvae at offshore and intermediate stations than at inshore stations. Gobies and the Pacific pompano, *Peprilus simillimus,* also occurred in all zones, but numbers of larvae represented were moderate. Larval saury occurred in both nearshore and offshore neuston tows, though they were somewhat more frequent in the latter.

Engraulis mordax exhibits the widest areal and temporal distribution of any larvae sampled, occurring not only on every cruise but at most stations as well. Greatest abundances of larvae appeared in March and June. CalCOFI data show abundance of larvae to be greatest from January through June (Kramer and Ahlstrom 1968). Other kinds of larvae occurring throughout the year in SCBS samples include *Sebastes* spp., *Citharichthys* spp., *Argyropelecus* spp., *Paralichthys californicus,* Atherinidae, and the gobies.

Larvae that occurred most often in June and September were *Hypsoblennius* spp., *Paralabrax* spp., *Sphyraenna argentea* (Pacific barracuda), *Oxyjulis californica* (señorita), *Peprilus simillimus, Trachurus*

TABLE 3
Geographical and Seasonal Distributions of Selected Taxa, Given as Numbers of Larvae per 10m² Sea Surface in Oblique Tows

Season	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore	Nearshore	Intermediate	Offshore
A. Taxa with offshore larvae									
	Stenobrachius leucopsarus			*Leuroglossus stilbius*			*Bathylagus ochotensis*		
Sept.-Oct.	0	0	0.3	0	0	0	0	0	0.1
Dec.-Jan.	4.5	4.8	18.3	0.1	65.3	125.7	0	5.2	24.7
Feb.-Mar.	20.3	161.5	70.3	0.3	43.8	133.2	0.4	5.4	6.1
June	0	3.6	3.3	0	3.1	2.0	0	0.8	0.9
	Merluccius productus			*Trachurus symmetricus*			*Triphoturus mexicanus*		
Sept.-Oct.	0	0	0.2	0	1.7	2.3	0.6	5.7	6.0
Dec.-Jan.	0.7	4.6	74.2	0	0	0	0	0	0
Feb.-Mar.	0	13.8	51.6	0	0	0	0	0	0
June	0	0	0	0.5	0	0.6	0.6	0.8	1.5
	Argyropelecus spp.			*Protomyctophom crockeri*			*Tarletonbeania crenularis*		
Sept.-Oct.	0	0.5	1.9	0	0.5	1.0	0	0.2	1.2
Dec.-Jan.	0	1.0	2.7	0	0	0.5	0.2	0.7	1.8
Feb.-Mar.	0	1.5	3.3	0	0	1.3	0	0.9	0.5
June	0	1.6	0.3	0	0	0.5	0	0	0.5
B. Taxa with nearshore larvae									
	Genyonemus lineatus			*Paralichthys californicus*			*Sardinops caeruleus*		
Sept.-Oct.	0.6	0	0	8.7	2.1	0.5	6.9	0.5	0
Dec.-Jan.	25.6	36.7	0.5	4.1	1.4	0	0.1	0	0
Feb.-Mar.	102.5	62.7	10.8	5.5	5.2	0.5	0.2	0	0
June	0	0.8	0	2.1	1.6	0.3	0	0	0
	Hypsoblennius spp.			*Paralabrax* spp.			*Seriphus politus*		
Sept.-Oct.	13.1	1.2	0.3	2.9	12.5	2.1	6.5	1.2	0
Dec.-Jan.	0.2	0	0	0	0	0	0.2	0	0
Feb.-Mar.	0	0	0	0.2	0	0	0	0	0
June	2.5	3.0	0.3	4.4	2.4	0.1	11.6	3.5	0
	Pleuronichthys ritteri			*Pleuronichthys verticalis*					
Sept.-Oct.	2.6	0	0	2.1	1.9	0			
Dec.-Jan.	0.7	0	0	1.3	0	0			
Feb.-Mar.	0.3	1.9	0	7.2	7.6	1.9			
June	0	0	0	4.9	3.2	0			
C. Taxa with cosmopolitan larvae									
	Engraulis mordax			*Sebastes* spp.			*Citharichthys* spp.		
Sept.-Oct.	41.0	118.5	73.0	1.6	11.7	2.9	3.0	17.9	5.9
Dec.-Jan.	840.0	214.1	238.4	21.3	29.3	104.6	2.9	3.7	13.8
Feb.-Mar.	490.0	1,567.8	3,074.4	7.0	196.4	94.8	0.6	8.7	3.7
June	1,191.1	1,343.7	167.5	0.4	7.5	7.7	1.4	2.8	1.2
	Gobiidae			*Peprilus simillimus*					
Sept.-Oct.	1.0	1.3	0.5	1.0	2.5	1.1			
Dec.-Jan.	4.7	0.4	0.5	0	0	0			
Feb.-Mar.	0.7	0.5	1.2	0	0	0			
June	0.8	1.2	1.0	8.1	4.6	4.3			

Each seasonal grouping is based on two or three different cruises. The geographical grouping ''nearshore'' includes the 44 samples from all X01 and X02 stations, 303, and San Onofre (see Table 1); ''intermediate'' includes the 20 samples from stations 103, 203, and 304; and ''offshore'' includes the 48 samples from all X05 and X06 stations.

symmetricus, and *Triphoturus mexicanus*. Larval saury were found in every season except winter.

Some of the larvae could be placed into recurrent groups. For the data from neuston tows, we chose an affinity level of $\geqslant 0.3$ as the criteron for grouping. Group N1 (Figure 1) occurred, as a group, in winter and spring primarily at nearshore stations, in spite of the fact that *Engraulis* and the *Sebastes* spp. category were cosmopolitan in distribution (Table 3). Somewhat surprisingly, the three affiliated categories, though themselves of nearshore origin, had higher affinities with the cosmopolites than with *Genyonemus*. Group N2 occurred only six times, in summer and fall, most often at offshore stations; larval saury *(Cololabis)* were found in spring as well.

Taxa from the oblique tows were grouped using an affinity level of $\geqslant 0.5$. Group O1 (Figure 2) included two offshore larvae (Table 3) and two cosmopolites, and the 34 occurrences as a group were mainly at offshore stations in winter, spring, and summer (Figure 3). Within these 34 occurrences, all of the six possible correlations in abundance were positive, and five were significantly so ($p < 0.05$), which means that the populations constituting the group were cohesive; the times and places that were ''best'' or ''worst'' (in terms of abundance) for one population

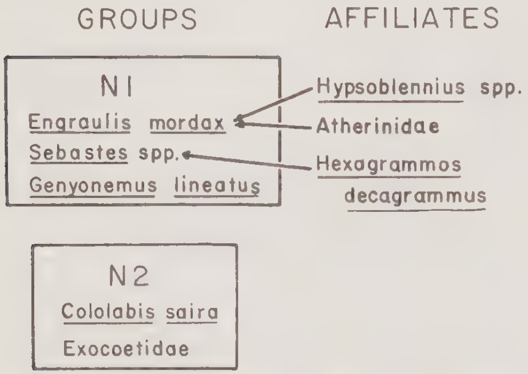
GROUPS
AFFILIATES
N1
Engraulis mordax
Sebastes spp.
Genyonemus lineatus
Hypsoblennius spp.
Atherinidae
Hexagrammos decagrammus
N2
Cololabis saira
Exocoetidae

Figure 1. Recurrent groups of larval fish in neuston tows in the Southern California Bight. An affinity index of ⩾0.3 is the criterion for grouping. "Affiliates" are those categories having significant affinity with some but not all members of a group, as indicated by arrows.

tended also to be best or worst for all other members of the group. The cosmopolitan flatfish *Citharichthys* was affiliated with the cosmopolitan members of the group, as was the offshore *Bathylagus* with the offshore members.

Group O2 was found exclusively at nearshore stations, and occurred as a group only in summer and fall (Figure 3); this group seems superficially similar to Group O3 in geographic distribution, and the two complete groups occurred together in four of ten possible cases. The members of Group O2 were not particularly coherent in abundance, since there were a positive, a negative, and a zero correlation between the pairs at the ten stations where the group occurred.

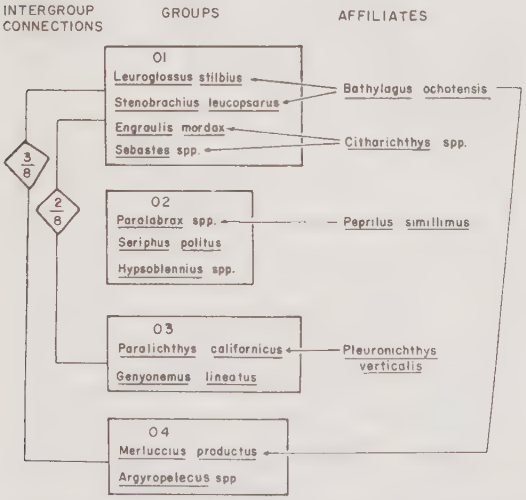
INTERGROUP CONNECTIONS
GROUPS
AFFILIATES
O1
Leuroglossus stilbius
Stenobrachius leucopsarus
Engraulis mordax
Sebastes spp.
Bathylagus ochotensis
Citharichthys spp.
3/8
2/8
O2
Paralabrax spp.
Seriphus politus
Hypsoblennius spp.
Peprilus simillimus
O3
Paralichthys californicus
Genyonemus lineatus
Pleuronichthys verticalis
O4
Merluccius productus
Argyropelecus spp

Figure 2. Recurrent groups of larval fish in oblique tows in the Southern California Bight. An affinity index of ⩾0.5 is the criterion for grouping. "Intergroup connections" indicates the proportion of all possible affinities (the denominator) that were actually realized (the numerator) between pairs of categories whose members were in different groups. "Affiliates" are those categories having significant affinity with some but not all members of a group, as indicated by arrows.

The principal difference between Group O2 and Group O3 was seasonal: the latter group was found in winter and spring as well as fall (Figure 3), and occurred only once (out of 27 times) in summer. The abundances of its two members were positively correlated in the 27 occurrences, but not significantly so.

Group O4 was found offshore, and in fact was combined with Group O1 when an affinity level of 0.4 was used for grouping. It was even more strictly offshore than was Group O1, and only one of 17 occurrences as a group was outside the period between January and March. Its two members had significant, positive correlations in abundances in the 17 occurrences of the group.

When recurrent groups were established with an affinity level of 0.4 as the criterion, an additional

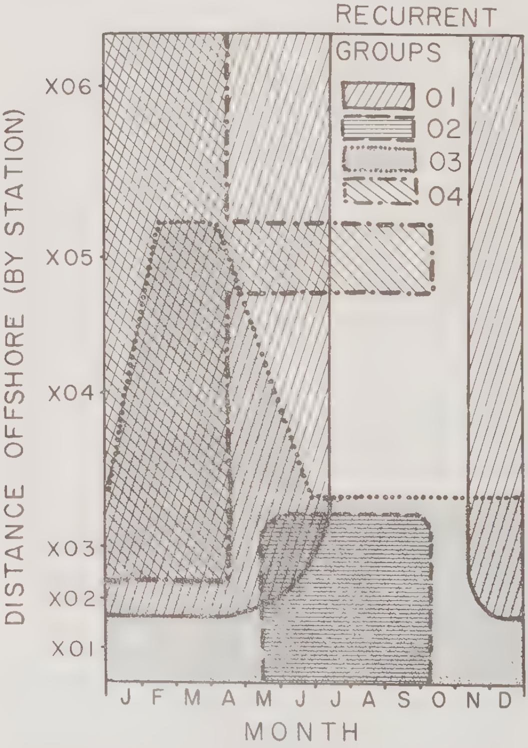

Figure 3. Areal and seasonal distributions of the recurrent groups in oblique tows (see Figure 2). Contour lines enclose all stations at which the entire group occurred. "X" on the ordinate equals 1, 2, or 3; see Table 1 for locations and depths of stations. The 300-m contour and 10-km distance offshore both occur between X03 and X04.

offshore, summer-fall group consisting of *Trachurus symmetricus* and *Triphoturus mexicanus* was found. A second group—*Lyopsetta exilis* (slender sole) and *Parophrys vetulus* (English sole)—was found only in March and at stations an intermediate distance from shore.

DISCUSSION

We have expressed results of oblique tows as catch per 10 m^2 sea surface; this rests on the assumption that the full depth range for fish eggs and larvae was sampled. Studies in the California Current region indicate that most fish eggs and larvae are distributed within the upper mixed layer or in the upper portion of the thermocline, between the surface and approximately 125 m, even in daytime (Ahlstrom 1959). Since most deep hauls averaged 210 m deep, the depth range for most eggs and larvae offshore was sampled. However, the interpretation of results from shallow stations is less sure, since the depth range for larvae and eggs has not been established and since the area on and just above the bottom was not sampled by our oblique hauls. It is likely (Brewer, Lavenberg, and McGowen, unpublished) that we would have found greater abundances of several nearshore larvae had we used an epibenthic net.

The question of vertical distribution also affects the interpretation of the recurrent groups. As mentioned earlier, a recurrent group consists of organisms that are frequently found in the same samples. Since our net tows integrated from the surface to 210 m at the offshore stations, it is possible that members of the same recurrent group have only minor ecological interactions, because they live at different depths. For example, larval *Engraulis, Sebastes* spp., *Citharichthys* spp., and *Stenobrachius* (formerly *Lampanyctus leucopsarus)* occur primarily in the mixed layer near the surface, while *Bathylagus, Leuroglossus,* and *Merluccius* occur below the thermocline (Ahlstrom 1959). Hence a recurrent grouping based on vertical distributions probably would separate *Leuroglossus* from the other members of Group O1.

Brewer, Lavenberg, and McGowen (unpublished) sampled the inshore waters of the Southern California Bight in spring and fall of 1978. The most significant faunal difference between their results and those reported here was the occurrence of large numbers of larval chub mackerel *(Scomber japonicus),* rivaling *Engraulis* for dominance, in June of 1978.

The analysis of the recurrent groups in the oblique tows amplified the tabulation of geographic distributions (Table 3) by indicating subgroups within the basic distinction between nearshore and offshore occurrences. Differences in season of occurrence separated groups that seemed geographically similar, and there was no specifically cosmopolitan group.

A recent study off the coast of Oregon (Richardson and Pearcy 1977) demonstrated clear division of larval fish into an inshore group (the shoreward 28 km, water 100 m deep or less) and an offshore group (37-111 km, water >100 m), with a transition zone where larval fish were rare. Very few species were cosmopolites, and this is perhaps not surprising in view of the relatively simple bathymetry and predominantly longshore transport along the Oregon coast. In the Southern California Bight a complex gyral circulation and a series of deep basins between the coast and the chain of offshore islands and banks make patterns of distribution less clear.

The anchovy *Engraulis* occurred in the offshore assemblage of Oregon and was not as abundant as *Sebastes* spp. and the myctophids *Stenobrachius leucopsarus* and *Tarletonbeania crenularis*. Also, larval anchovy were very seasonal in occurrence off Oregon (June-August), unlike the situation in the Southern California Bight. As in the SCBS collections, *Sebastes* and *Stenobrachius* were found off Oregon in most months, but the season of greatest abundance was the late spring rather than winter and early spring.

A further study off the Oregon coast, based on many transects in the springs of four years, revealed a persistent pattern of two or three coastal assemblages, a transitional assemblage, and one or two offshore assemblages, with the coastal/offshore separation generally paralleling the shelf/slope break (Richardson, Laroche, and Richardson 1980). Minor variations from year to year in the locations of these assemblages may have been related to variations in the strength and direction of coastal winds. An important finding was that the geographical pattern of assemblages was relatively constant in spite of month-to-month and year-to-year variations in the abundances of the species dominating each assemblage, especially near the coast. These variations were not well correlated between species, so that a particular geographically defined assemblage might be dominated by different species in different months or years.

There are some ecological advantages for larvae that develop in the inshore zone. Recently, it has been demonstrated that first-feeding larval *Engraulis mordax* must occur with high concentrations of particles in the size range of large dinoflagellates in order to feed adequately (Lasker 1975). Characteristically, these regions exist close to shore off southern California, and relatively steep inshore-offshore gradients in planktonic stocks (as chlorophyll, primarily production, particulate organic carbon, etc.) have already been reported (Eppley, Sapienza, and Renger 1978).

Sardinops caeruleus, the Pacific sardine, occurred only near shore on SCBS cruises. Eggs and larvae of this species used to be taken over wide areas both inshore and offshore (Ahlstrom 1959a), but occurrence has changed primarily to inshore zones. It is likely that when breeding stocks were reduced, the remaining population tended to spawn selectively in areas of high productivity, where survival of larvae is enhanced. Thus, the inshore zone could be important for the recovery of certain overfished or otherwise depleted stocks, including the anchovy if its population were ever drastically reduced. It is important to verify the relation between depleted stocks and the productive inshore zone, since this zone is the most likely to be affected by anthropogenic perturbations.

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DISTRIBUTION AND MORTALITY OF NORTHERN ANCHOVY LARVAE IN 1978 AND 1979

ROGER P. HEWITT AND RICHARD D. METHOT, JR.
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Eleven ichthyoplankton surveys, conducted during the winter and spring quarters of 1978 and 1979, indicate that spawning of the northern anchovy, *Engraulis mordax,* was contracted both spatially and temporally in 1978 relative to 1979. Larvae were farther offshore in 1979. Instantaneous daily larval mortality rate estimated from slope of the age-frequency distribution (yolk sac through 15 mm, ca. 25-30 days) varied insignificantly between 1978 and 1979 and averaged 0.168. Comparison to a simple model of spawning suggests that seasonal changes in the slopes are due solely to a systematic bias and not to real changes in the mortality rate.

Seasonal larval production was compared with birthdate distributions of fish surviving to the juvenile stage. In both years March had the greatest larval production and was the commonest month of birth among the survivors of the larval stage. Larval survivorship tended to increase within the 1978 spawning season and decrease within the 1979 season. Low survivorship in winter 1978 is consistent with the hypothesis that winter storms disrupted aggregations of prey necessary for larval feeding, but does not explain why apparent recruitment was greater in 1978 than 1979. Variation in larval survivorship could not be attributed to larval mortality. The offshore distribution of larvae in 1979 may have contributed to the relatively low survival.

RESUMEN

Once estudios de ictioplancton realizados durante los trimestres de invierno y primavera en 1978 y 1979 indican que el desove de la anchoveta *Engraulis mordax* en 1978 se produjo relativo al de 1979, tanto espacialmente como temporalmente. Las larvas estaban más lejos de la costa en 1979. El indice de mortalidad instantánea diaria de larvas que se estimó de la inclinación de la distribución de frecuencias de edades (vitelo hasta 15 mm, alrededor de 25-30 días) varió insignificativamente entre 1978 y 1979, con un promedio de 0.168. Una comparación con un modelo simple de desove sugiere que cambios temporales en las inclinaciones se deben únicamente a un sesgo sistemático y no a cambios verdaderos en el indice de mortalidad.

La producción larval temporal fue comparada con distribuciones de fechas de nacimiento de peces que sobrevivieron hasta la etapa juvenil. En ambos años, la mayor producción de larvas occurrió en marzo, y el haber nacido en este mes era más común entre los sobrevivientes de la etapa larval. La supervivencia larval tendía a aumentar en la época de desove de 1978 y a descender en la época de 1979. La supervivencia baja del invierno de 1978 es consistente con la hipótesis de que tormentas de invierno interrumpieron conjuntos de presas necesarias para alimentar las larvas, pero no explica porqué el reclutamiento era mayor en 1978 que en 1979. La variación en la supervivencia larval no se pudo atribuir a la mortalidad larval. La distribución de larvas fuera de la costa en 1979 pudo haber contribuído a la supervivencia relativamente baja.

INTRODUCTION

The planktonic phase of a schooling fish's life history is considered the most amenable to quantitative sampling (Smith and Richardson 1977). Egg and larvae surveys have been used to estimate the number of adults responsible for their production (e.g., Sette and Ahlstrom 1948; Saville 1964; Smith 1972). Fish larvae are also of interest because they are the link between the present adult stock and some future recruitment to the adult stock. The lack of a clear relationship between stock and recruitment has focused attention on events during the larval stage and their ultimate effect on survival to the juvenile and adult stages.

The literature on the pelagic fishes of the California Current is particularly rich. Smith (1981) summarized the influences on northern anchovy larval survival: (1) the availability of suitable prey for larvae exhausting their yolk sacs (Lasker 1978); (2) interspecific and intraspecific predation (Hunter 1976; Hunter and Kimbrell 1981); (3) starvation (Hunter 1976; O'Connell 1980); (4) effect of adult nutritional state on quality of eggs and fitness of larvae (Smith and Lasker 1978; Hunter and Leong 1981); (5) preschooling dispersal (Smith 1973; Hewitt 1981); and (6) larval transport to or from favorable areas (Sette 1950; Parrish et al. 1981).

In this report we describe the results of ichthyoplankton surveys conducted in 1978 and 1979, and discuss what may be inferred about factors affecting larval anchovy survival during those 2 years. Distri-

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[Manuscript received March 1, 1982.]

bution maps, abundance estimates, and mortality are reported for each of 11 surveys.

METHODS AND MATERIALS

The data presented here were obtained during 11 cruises (Table 1) conducted off the coast of the Californias (Figure 1) in 1978 and 1979, as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Plankton samples were taken obliquely from a depth of 210 m with 0.505-mm mesh nylon nets mounted on a bongo frame (see Kramer et al. 1972, for detailed methodology). Samples were preserved in a buffered Formalin solution and an ethyl alcohol solution. A subsample of the alcohol-preserved specimens of anchovy larvae was aged using daily increments in the otoliths (Methot 1981). Anchovy larvae in Formalin-preserved samples were enumerated in 1-mm classes of standard length. Preserved larval lengths were adjusted to live lengths using the shrinkage factors reported by Theilacker (1980).

We use two different summarization procedures. The first will be presented on a fine spatial scale but will not take into account extrusion, avoidance, and growth that affect the relation between larval production and the catch in each 1-mm size class. The results of this first summarization are used to describe the distribution and relative abundance of larvae. The second procedure incorporates factors affecting the relation between larval production and catch but requires a large sample size, so no within-cruise stratification was possible. The age-specific larval productions resulting from the second summarization are used to calculate mortality rates of larvae.

Only samples from the central population of anchovy are considered in the quantitative analyses. Electrophoretic and morphometric data indicate that anchovy along southern Baja California constitute a separate population (Vrooman and Smith 1971). We exclude samples collected south of CalCOFI line 110 (Figure 1). A third population occurs primarily along the coasts of Oregon and Washington.

TABLE 1
CalCOFI Surveys 1977 through 1979

Cruise	Dates	Number of stations occupied	% positive for anchovy larvae
7712	Dec 8-Dec 19	80	54
7801	Jan 5-Jan 31	211	46
7803	Feb 18-Mar 15	208	59
7804	Mar 29-Apr 25	147	48
7805	May 14-Jun 10	132	39
7807	Jun 20-Jul 17	219	23
7808	Jul 31-Aug 26	118	17
7901	Jan 12-Jan 22	46	67
7903	Feb 25-Mar 13	95	66
7904	Apr 1-Apr 17	61	54
7905	Apr 30-May 21	102	51

In the first summarization, larval catches were stratified into four classes of live length (2.6-4.9 mm, 5.0-8.3 mm, 8.4-11.3 mm, and 11.4-14.3 mm) and expressed as numbers of larvae under 10 m^2 of sea surface. Distribution maps of these summarized data were prepared. Each station's contribution to the larval census was weighted by the distance to adjacent stations along the CalCOFI line. Offshore stations were 40 miles apart; inshore stations were as close as 4 miles. The weighted sum of larvae was calculated for each line. Sums of unsampled lines were extrapolated from sums in adjacent lines and cruises. The total of the sums for CalCOFI lines 60-110 was the cruise's larval census.

Each station's contribution to the mean distance offshore of larvae was weighted by the distance to adjacent stations and by the catch of larvae at the station.

The second summarization procedure fits a negative binomial weighted model (Bissell 1972) to the frequency distributions of each 1-mm length class. The procedure was adapted for use on fish larvae by Zweifel and Smith (1981). The negative binomial distribution is described by two parameters: the mean, m; and the contagion parameter, k. The variance is related to these parameters by:

$$\mathrm{Var} = m + \frac{m^2}{k}$$

According to the weighted model, the frequency distribution of actual catches depends not only on the underlying m and k but also on the individual effective sampler volume w_i. We consider two factors affecting each sample: volume of water filtered per unit depth and avoidance of the net by larger larvae during the day (Smith 1972). We include a third factor, extrusion of small larvae through the mesh, to permit quantitative comparison between size classes. This extrusion factor does not vary between samples. A fourth factor, temperature-and-month-dependent growth rate, corrects for variation in the period larvae remain in each size class. This duration factor transforms the results from a standing crop in each size class to production or flux through the size class. Each of the above factors is defined to be typically about 1.0. The product of the 4 factors is the effective sample volume w_i, for the i^{th} sample.

The correction for volume of water filtered was calculated as:

$$f_1 = \left(\frac{V}{D}\right)\frac{1}{3.5}$$

where V is volume filtered, D is maximum depth sampled, and 3.5 is the standard sample of 3.5 m^3 per m of depth.

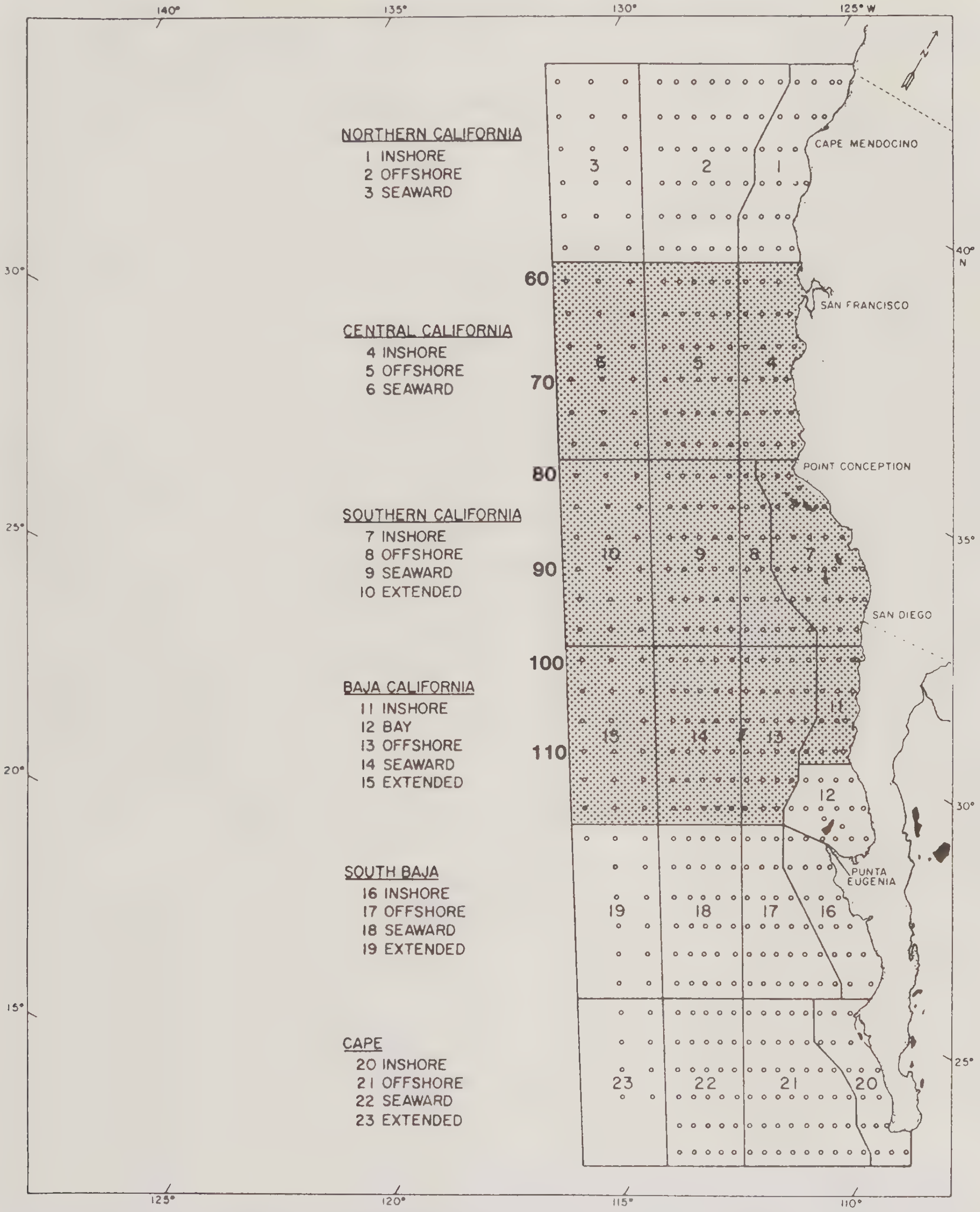

140°
135°
130°
125° W
N
NORTHERN CALIFORNIA
1 INSHORE
2 OFFSHORE
3 SEAWARD
CAPE MENDOCINO
40° N
30°
60
SAN FRANCISCO
CENTRAL CALIFORNIA
4 INSHORE
5 OFFSHORE
6 SEAWARD
70
80
POINT CONCEPTION
SOUTHERN CALIFORNIA
7 INSHORE
8 OFFSHORE
9 SEAWARD
10 EXTENDED
25°
35°
90
SAN DIEGO
100
BAJA CALIFORNIA
11 INSHORE
12 BAY
13 OFFSHORE
14 SEAWARD
15 EXTENDED
110
20°
30°
PUNTA EUGENIA
SOUTH BAJA
16 INSHORE
17 OFFSHORE
18 SEAWARD
19 EXTENDED
15°
CAPE
20 INSHORE
21 OFFSHORE
22 SEAWARD
23 EXTENDED
25°
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
125°
120°
115°
110°

Figure 1. CalCOFI survey grid is divided into 23 regions. The central subpopulation of the northern anchovy is contained within the shaded regions (Vrooman and Smith 1971).

The correction for avoidance of the net during daylight was calculated by a sinusoidal function:

$$f_2 = \frac{(1 + DN_L)}{2} + \frac{(1 - DN_L)}{2} \cos\left(\frac{2\pi t}{24}\right)$$

where DN_L is the midday-to-midnight catch ratio of L-length larvae, and t is the hour of the tow. The factor is 1.0 at midnight and declines to a size-specific minimum DN_L, at noon. The ratios of mean catch during night (2030-0230 h) to mean catch during day (0830-1630 h) are presented in Figure 2 along with similar curves derived from catches by the 1-m bridled net (Ahlstrom 1954; Smith 1981).

The correction for extrusion of small larvae through 0.505-mm mesh was calculated as:

$$f_3 = 0.3311 \exp\left\{ 1.10526[1\text{-}\exp(-0.0165L^3)] \right\}$$

where L is the preserved length of the larvae. This correction was derived by Zweifel and Smith (1981) from the catch rates of nets with 0.333-mm mesh compared to paired catches by 0.505-mm mesh. The factor increases asymptotically to 1.0.

The correction for duration of each size class was calculated from temperature-specific growth of yolk-sac larvae (2.6-4.1 mm) in the laboratory (Zweifel and Lasker 1976; Zweifel and Hunter, unpubl. data) and growth of feeding larvae measured in the sea by daily increments in otoliths (Methot and Kramer 1979). Methot (1981) found that growth was similar to temperature-specific growth in the laboratory, but a month-specific model, which we use here (Methot and Hewitt 1980), was a more precise description. We divide the durations by a standard duration of 2 d/mm.

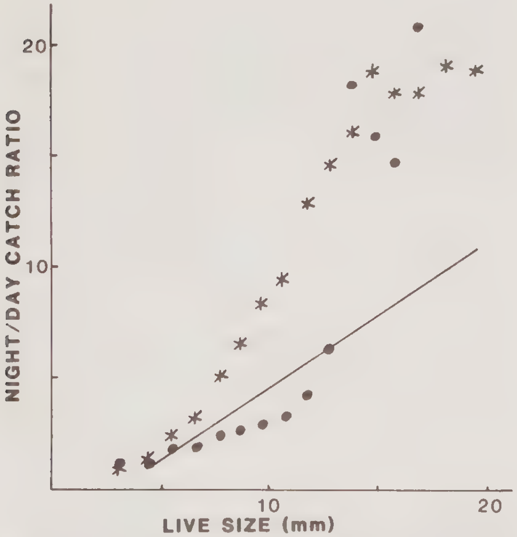


Figure 2. The night/day larval catch ratio increases with larval length. The dots were calculated from the 1978 and 1979 surveys using the bridle-free bongo net. The stars are similar ratios for anchovy larvae using the bridled 1-m net (Smith 1981). The solid line is a regression fit to the night/day catch ratios for sardine larvae using a bridled 1-m net (Ahlstrom 1954).

The slope of the relation between larval production (duration-corrected mean larval abundance) and age is an estimate of larval mortality rate. We calculate the linear regression of $\log_e$ (production) on age:

$$\log_e (m_t) = \log_e (m_o) - z(t)$$

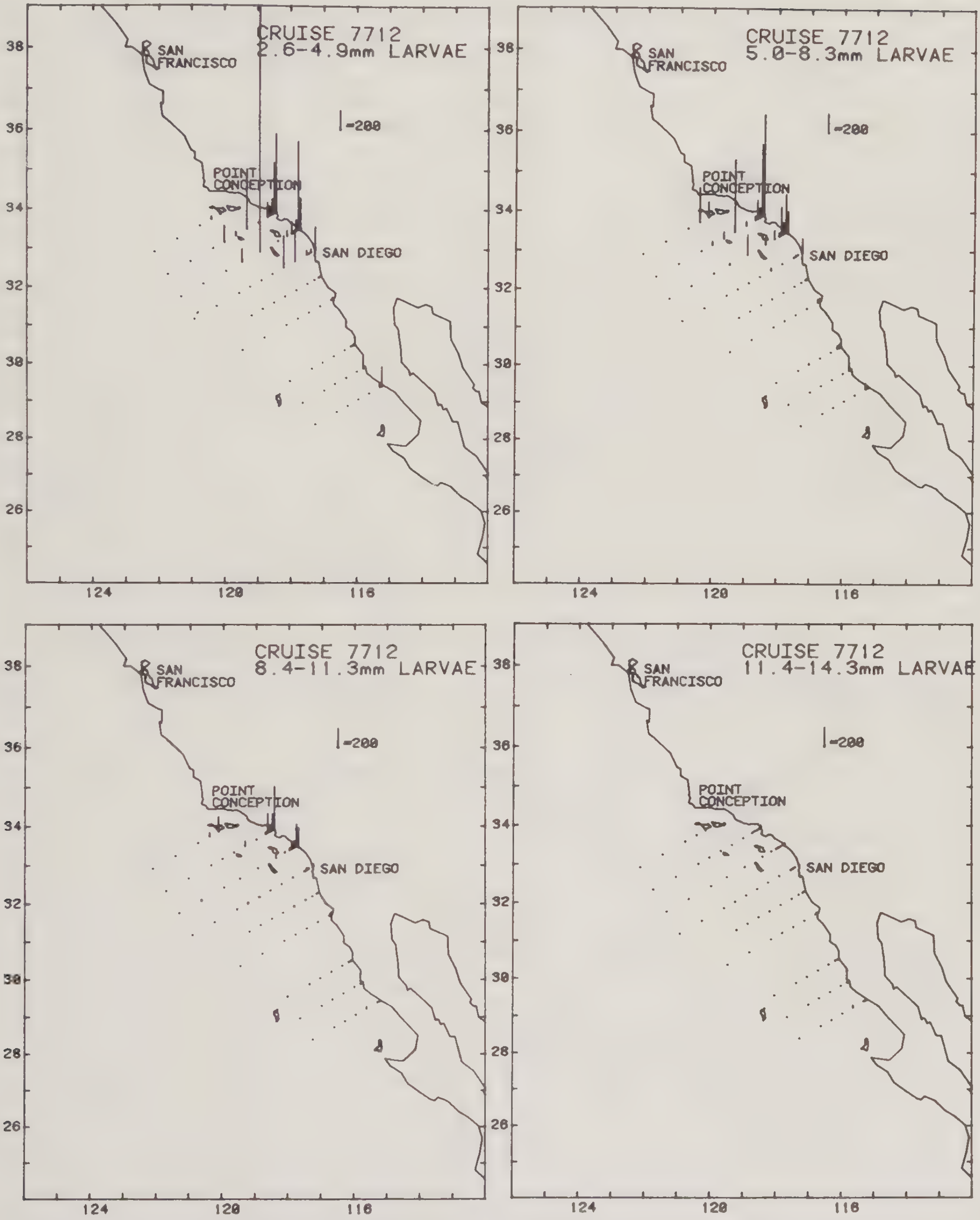
Where m_t is the mean production of the size class with mean age t, z is the instantaneous mortality rate, and m_o is the estimated production rate of hatching larvae (per 2 days). Interpretation of the slope as the mortality rate requires the assumption that the spawning rate is constant. Later we evaluate consequences of violating this assumption.

Hewitt (1982) makes use of patchiness indices derived from the contagion parameter, k.

Some selection of stations was necessary for the second summarization procedure. Samples with no larvae presented a problem because they cannot be clearly interpreted: some result from sampling outside the habitat entirely, and others result from low densities within the habitat. The zero samples do not influence the census estimates, but they do influence the fit of the negative binomial model to the frequency distribution of larval catch for each size class. We defined the habitat as those areas where a larva of any size was found, and excluded samples containing no larvae. In the Los Angeles Bight (Pt. Conception to San Diego), and within 20 miles of the coast, sampling effort was often increased. To correct for the effect of oversampling, data from up to 6 stations on the inshore end of a station line were averaged to a composite station.

RESULTS

The geographic distribution of spawning differed between the 2 years. In 1978 larvae were found throughout the surveyed region, but most occurred between Pt. Conception and San Diego (Figures 3-9). During May to August all larvae of the central population were in this subregion. In 1979 the distribution of spawning was displaced southward (Figures 10-13). In the region north of Pt. Conception (CalCOFI lines 60-77) the census of 2.6-4.9-mm larvae for the 4 cruises between January and May was 587 in 1978 and 109 in 1979 (Tables 2 and 3). In the region including lines 80-97 the censuses were 19,853 in 1978 and 13,240 in 1979. In the south, lines 100-110, only 2 cruises, March and May, can be compared. In 1978 the census for 2.6-4.9-mm larvae in March and May was 418; in 1979 it increased to 6258.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2.6-4.9mm LARVAE
CRUISE 7712
5.0-8.3mm LARVAE
CRUISE 7712
8.4-11.3mm LARVAE
CRUISE 7712
11.4-14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
=200
38
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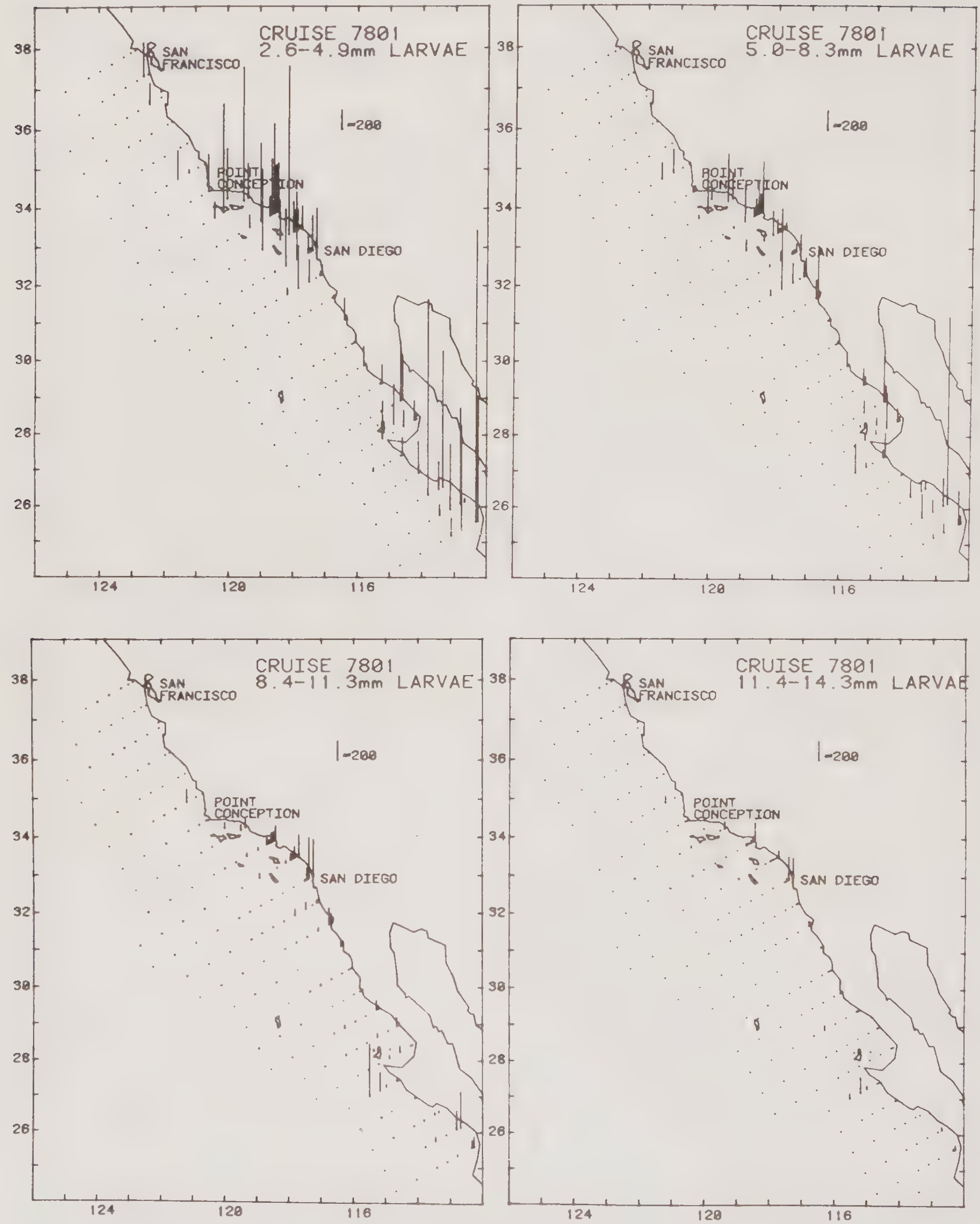
120
116

Figures 3 through 13. "Orchard" charts depict spatial disposition of four groups of larvae for each cruise. Height of "tree" is proportional to the number of larvae per 10 m² of sea surface.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CRUISE 7801
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CRUISE 7801
8.4-11.3mm LARVAE
CRUISE 7801
11.4-14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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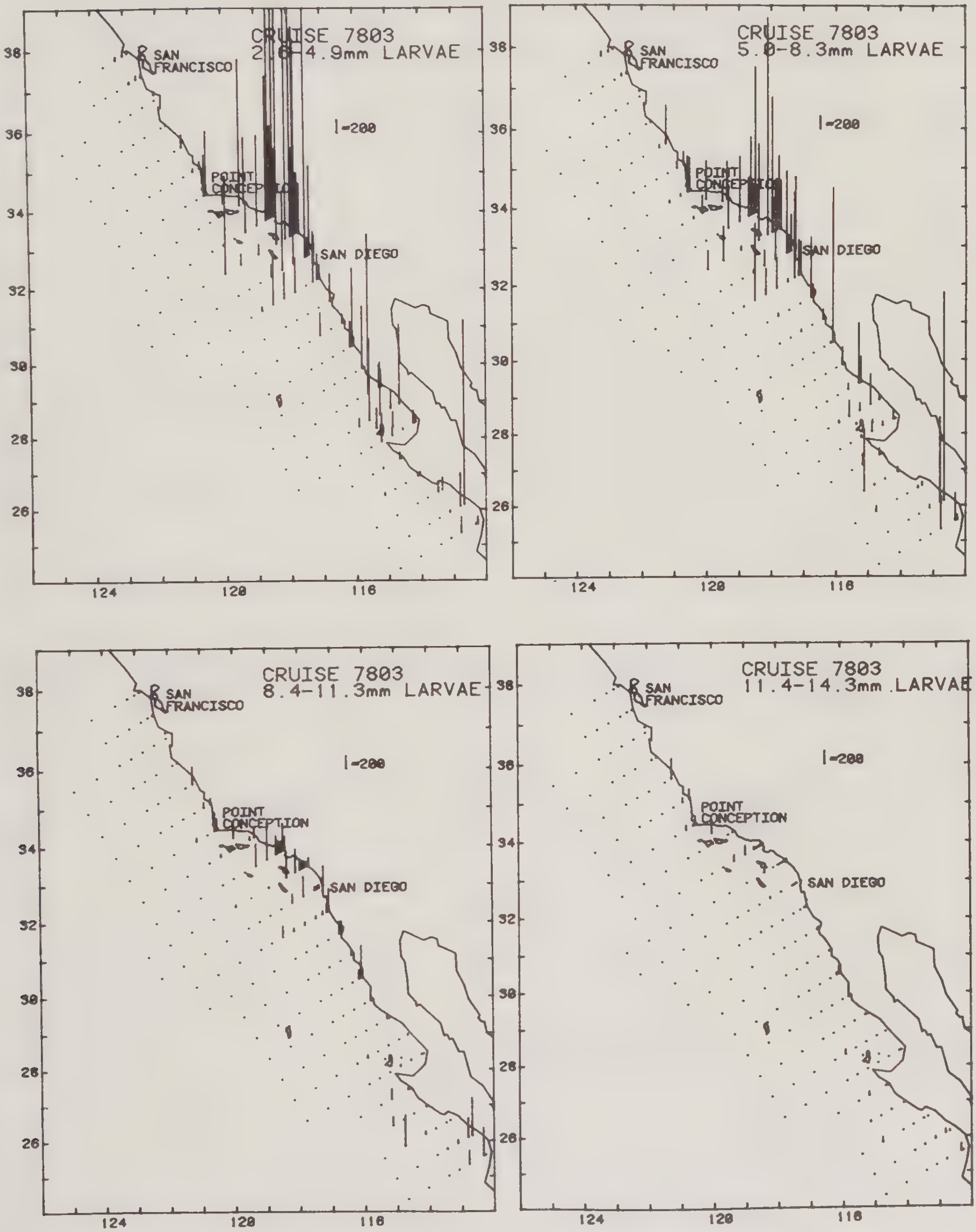
Figure 4.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POINT CONCEPTION
SAN DIEGO
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CRUISE 7803
5.0-8.3mm LARVAE
|=200
SAN FRANCISCO
POINT CONCEPTION
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CRUISE 7803
8.4-11.3mm LARVAE
|=200
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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CRUISE 7803
11.4-14.3mm LARVAE
|=200
SAN FRANCISCO
POINT CONCEPTION
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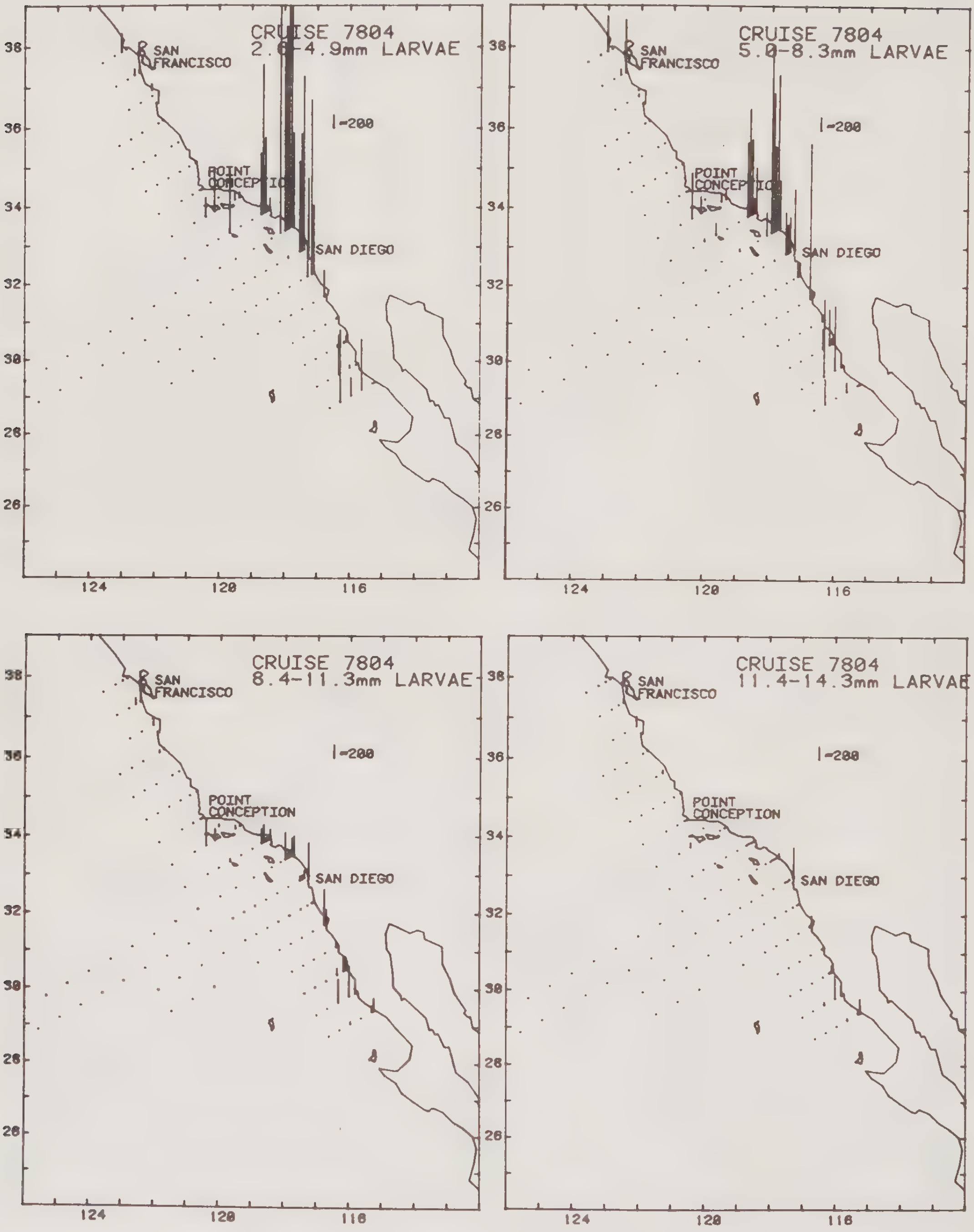
Figure 5.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CRUISE 7804
8.4-11.3mm LARVAE
CRUISE 7804
11.4-14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
|=200
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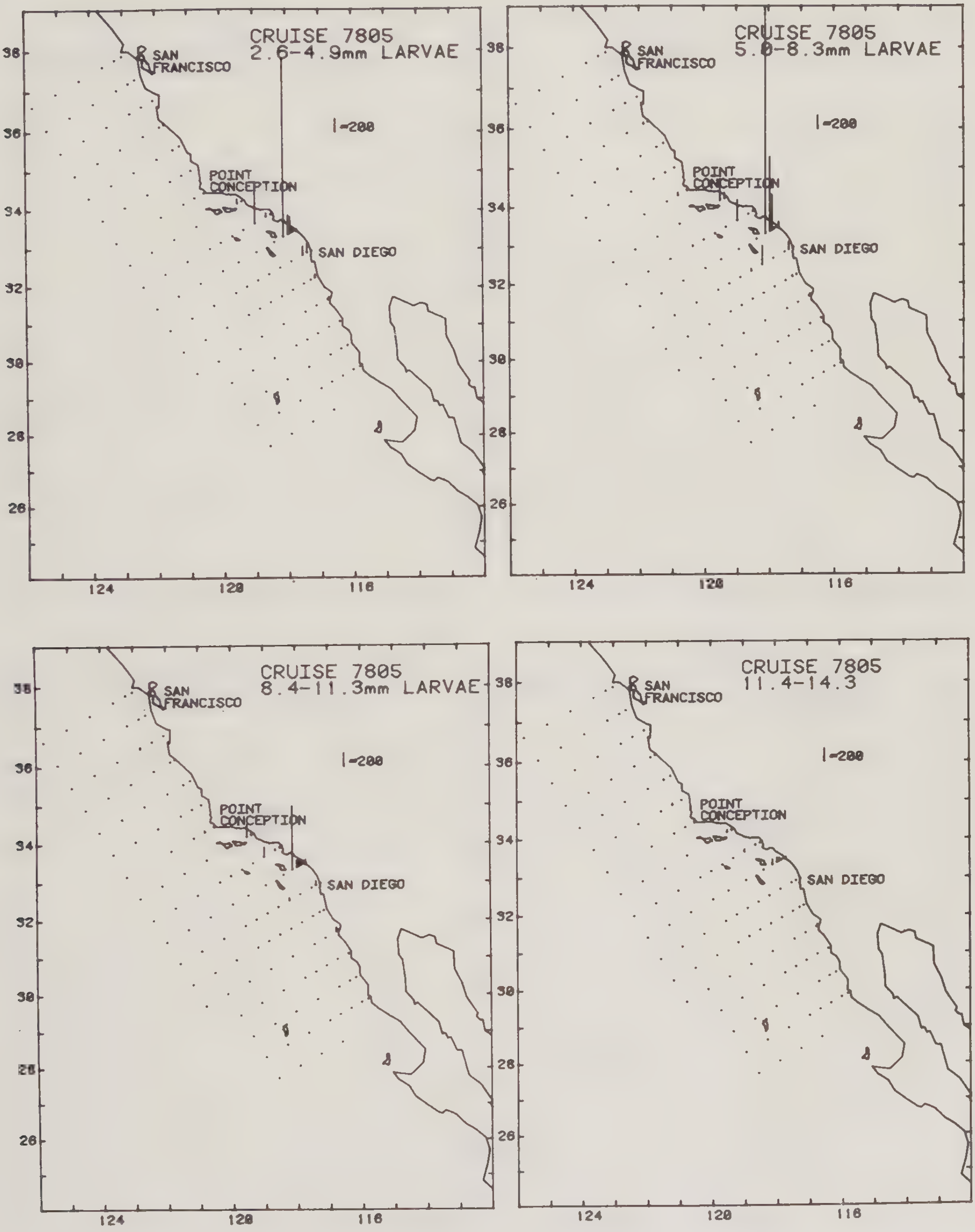
Figure 6.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CRUISE 7805
5.0-8.3mm LARVAE
CRUISE 7805
8.4-11.3mm LARVAE
CRUISE 7805
11.4-14.3
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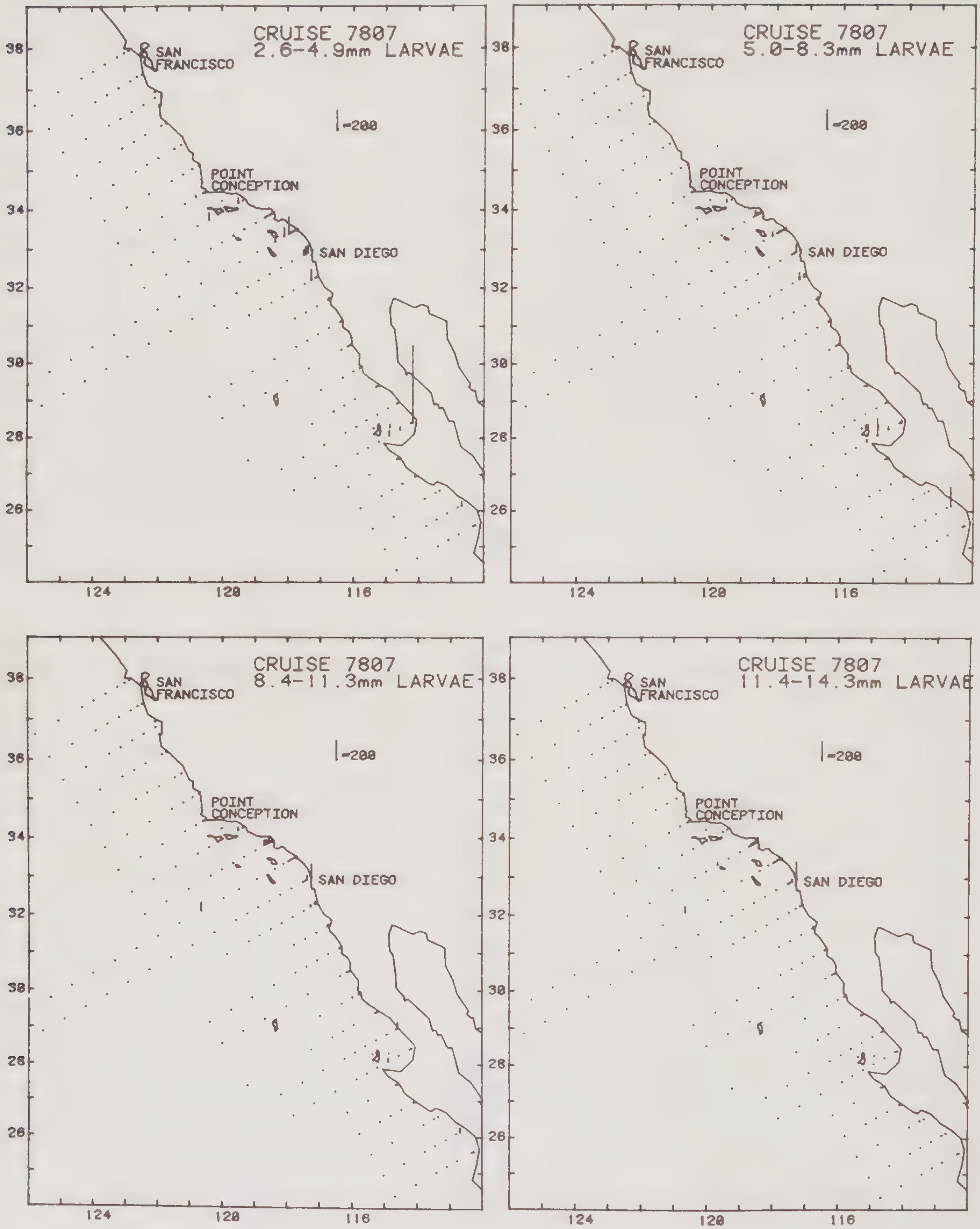
Figure 7.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CRUISE 7807
5.0-8.3mm LARVAE
CRUISE 7807
8.4-11.3mm LARVAE
CRUISE 7807
11.4-14.3mm LARVAE
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POINT CONCEPTION
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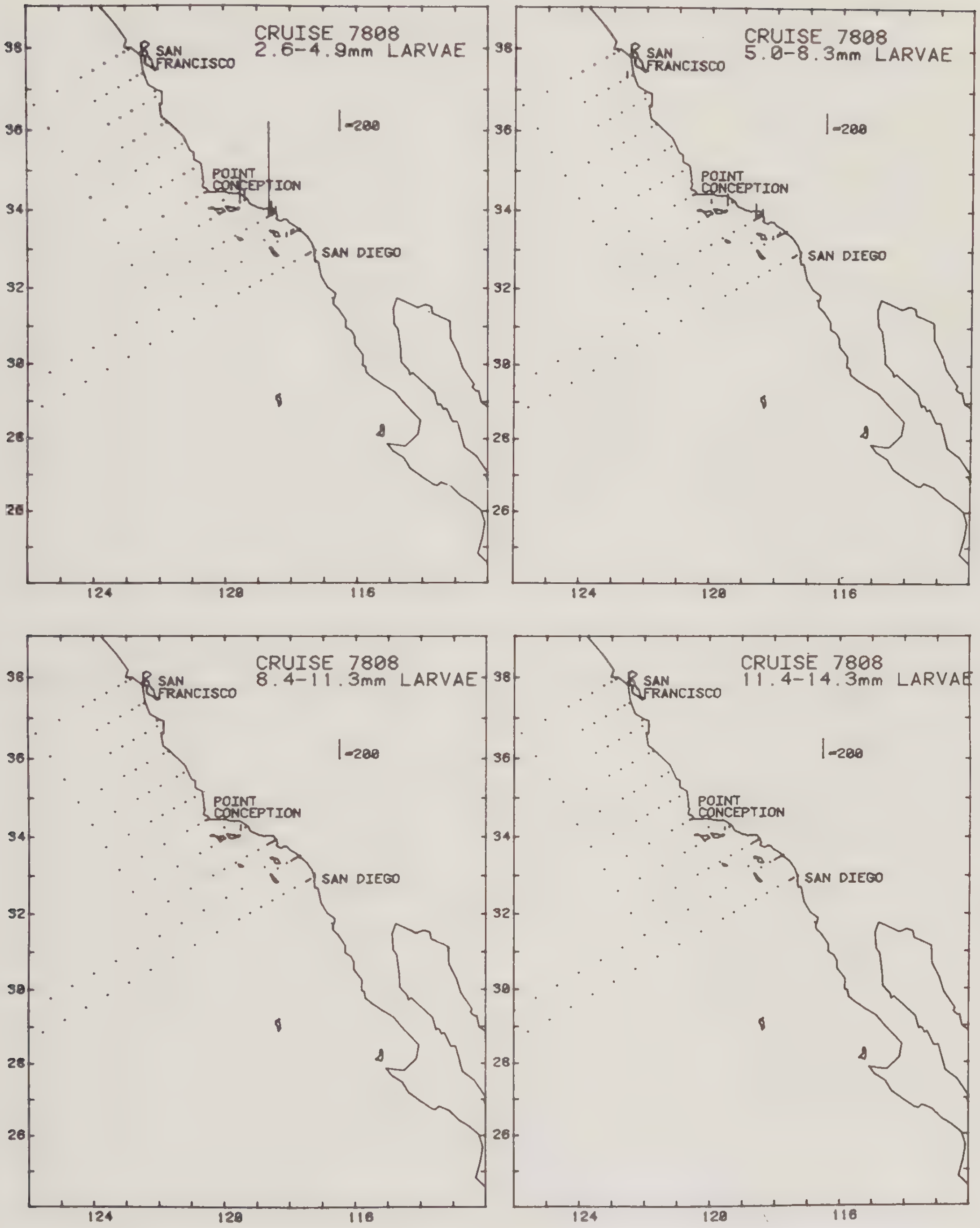
Figure 8.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CRUISE 7808
8.4-11.3mm LARVAE
CRUISE 7808
11.4-14.3mm LARVAE
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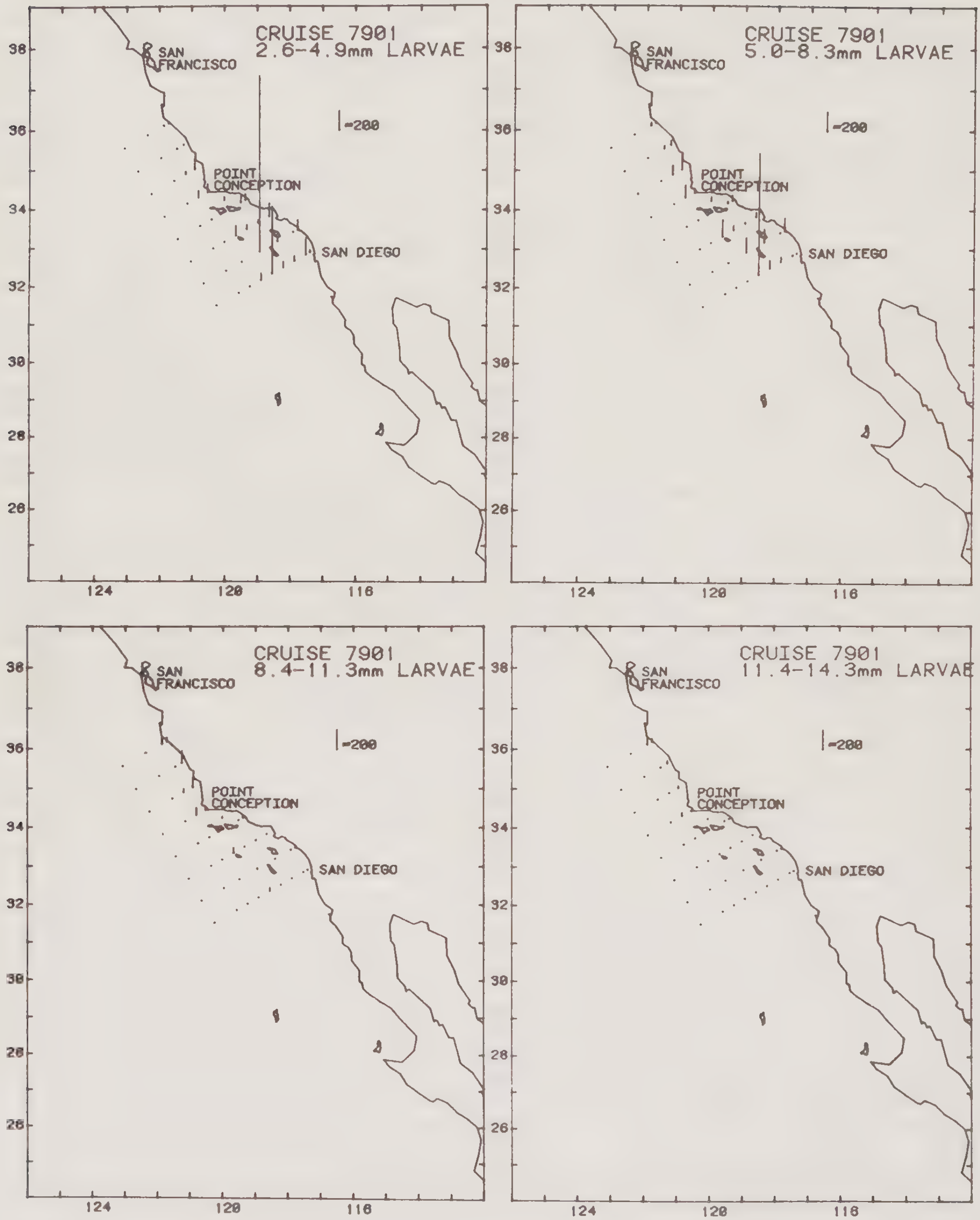
Figure 9.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CRUISE 7901
5.0-8.3mm LARVAE
CRUISE 7901
8.4-11.3mm LARVAE
CRUISE 7901
11.4-14.3mm LARVAE
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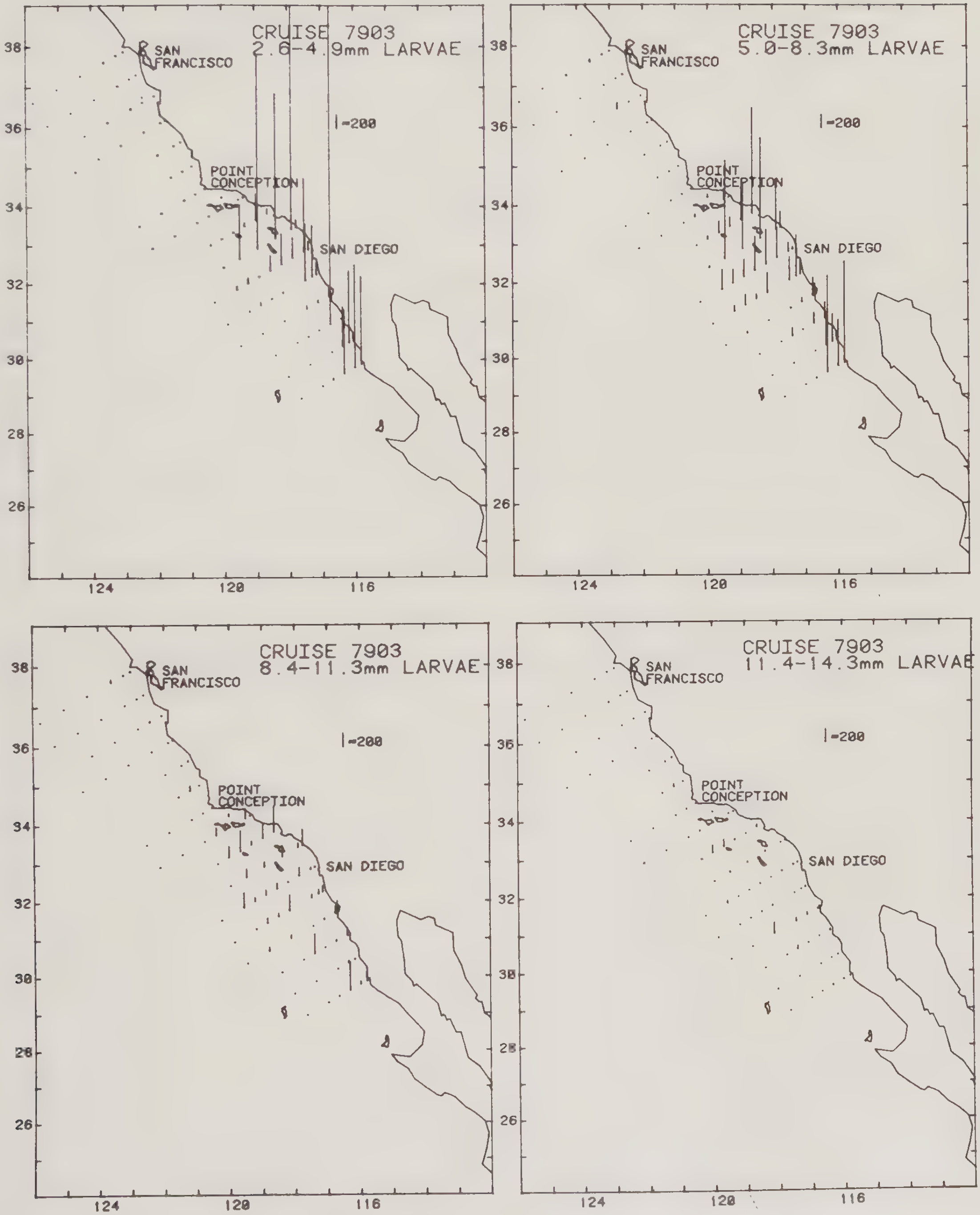
Figure 10.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CRUISE 7903
5.0-8.3mm LARVAE
CRUISE 7903
8.4-11.3mm LARVAE
CRUISE 7903
11.4-14.3mm LARVAE
SAN FRANCISCO
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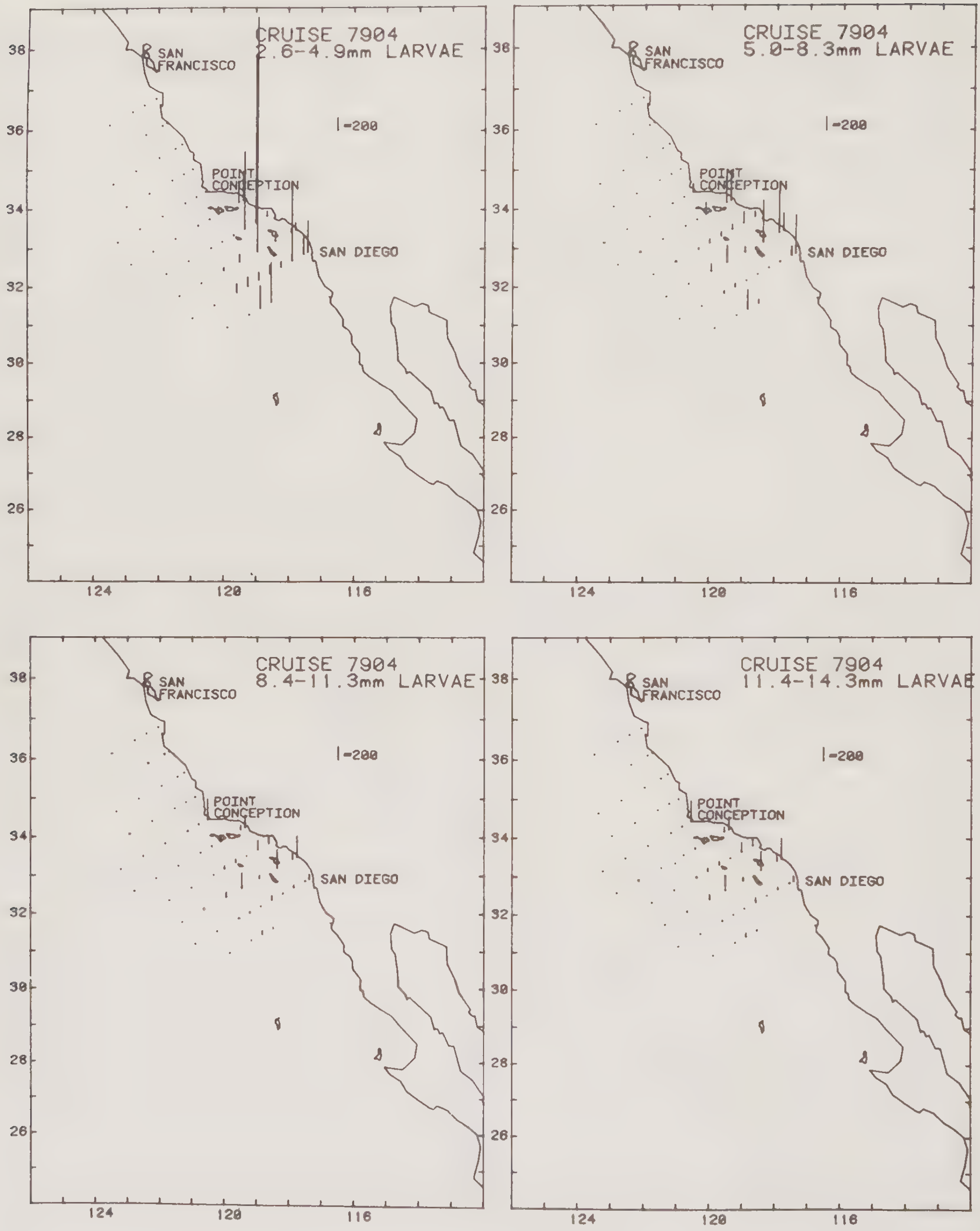
Figure 11.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CRUISE 7904
5.0-8.3mm LARVAE
CRUISE 7904
8.4-11.3mm LARVAE
CRUISE 7904
11.4-14.3mm LARVAE
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
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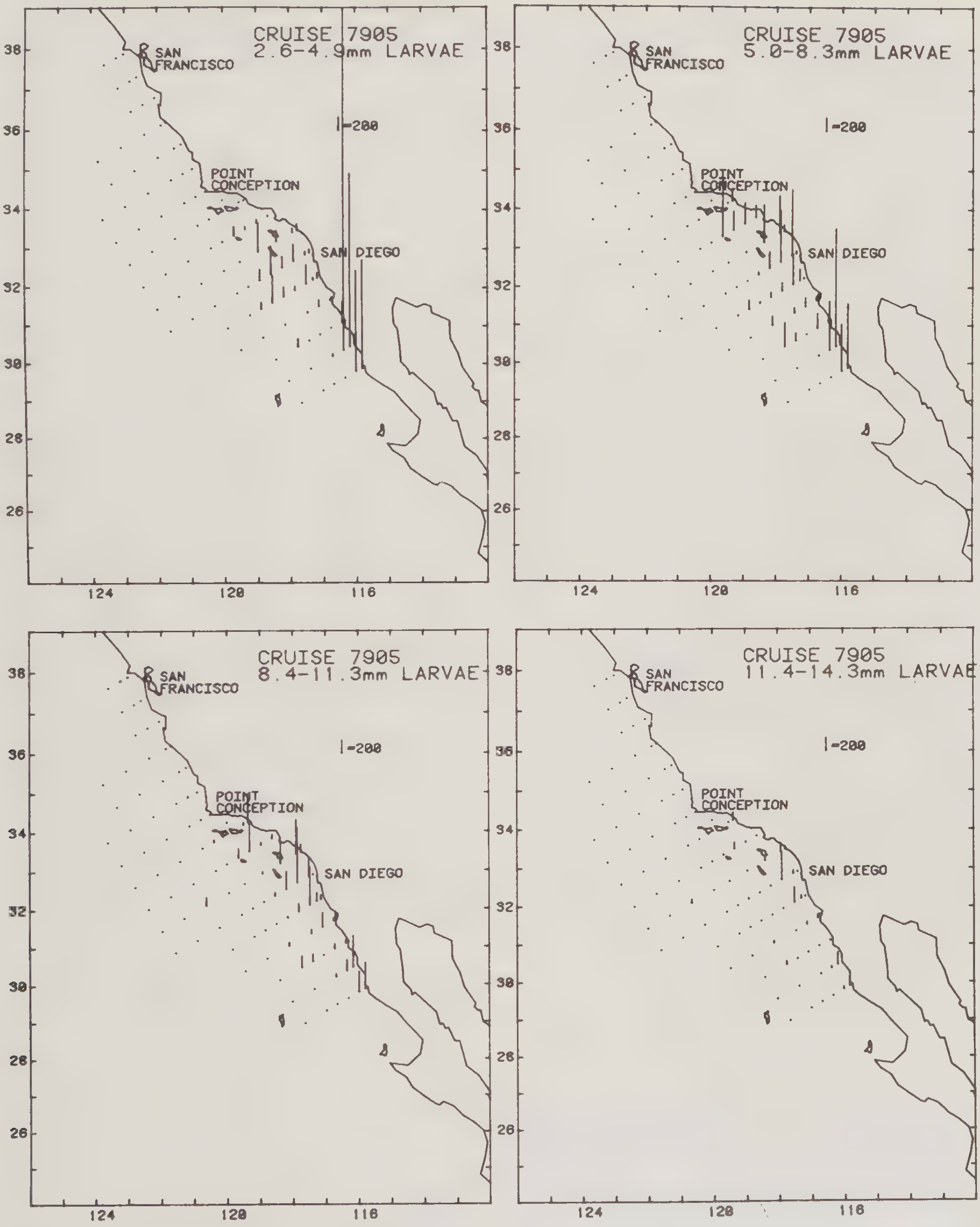
Figure 12.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CRUISE 7905
5.0-8.3mm LARVAE
CRUISE 7905
8.4-11.3mm LARVAE
CRUISE 7905
11.4-14.3mm LARVAE
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POINT CONCEPTION
SAN DIEGO
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Figure 13.

TABLE 2

Temporal and Spatial Distribution of Anchovy Larvae during 1978

Between lines	Size group	7712	7801	7803	7804	7805	7807	7808
60-70	2.6-4.9	(93)	110	44	77	0	0	0
	5.0-8.3	(44)	0	44	214	16	0	11
	8.4-11.3	(19)	5	16	110	16	0	0
	11.4-14.3	(0)	0	0	16	11	0	0
	Total	(159)	115	104	429	44	0	11
70-80	2.6-4.9	(93)	137	203	11	5	5	0
	5.0-8-3	(44)	121	264	11	27	0	0
	8.4-11.3	(19)	49	154	16	49	5	0
	11.4-14.3	(0)	22	115	11	33	5	0
	Total	(159)	324	814	49	181	22	0
80-90	2.6-4.9	2002	2156	9355	2574	737	110	170
	5.0-8.3	726	654	2755	1391	1023	33	66
	8.4-11.3	231	132	643	352	368	93	38
	11.4-14.3	5	38	104	22	60	66	11
	Total	3025	3129	13249	4609	2299	379	302
90-100	2.6-4.9	209	660	3283	1039	49	33	(0)
	5.0-8.3	27	429	1765	671	115	16	(0)
	8.4-11.3	5	137	346	148	44	16	(0)
	11.4-14.3	0	44	33	22	0	16	(0)
	Total	264	1369	5676	1969	236	104	(0)
100-110	2.6-4.9	16	165	418	203	0	0	(0)
	5.0-8.3	38	5	302	715	5	0	(0)
	8.4-11.3	5	49	93	308	5	0	(0)
	11.4-14.3	0	11	33	132	0	0	(0)
	Total	60	269	913	1485	11	0	(0)
60-110	2.6-4.9	2413	3129	13303	3904	791	148	170
	5.0-8.3	879	1209	5130	3002	1186	49	77
	8.4-11.3	279	372	1252	934	482	114	38
	11.4-14.3	5	115	285	203	104	87	11
	Total	3667	5206	20951	8541	2771	505	313

Values are x 10^9 larvae; parentheses denote extrapolated values.

TABLE 3

Temporal and Spatial Distribution of Anchovy Larvae During 1979

Between lines	Size group	7901	7903	7904	7905
60-70	2.6-4.9	(0)	16	0	0
	5.0-8.3	(22)	60	0	0
	8.4-11.3	(88)	33	0	0
	11.4-14.3	(66)	5	0	0
	Total	(198)	132	0	0
70-80	2.6-4.9	71	0	22	0
	5.0-8.3	132	0	55	0
	8.4-11.3	82	33	11	0
	11.4-14.3	27	16	0	0
	Total	319	49	93	5
80-90	2.6-4.9	968	3894	3003	374
	5.0-8.3	253	2805	1017	924
	8.4-11.3	49	544	544	671
	11.4-14.3	11	155	137	176
	Total	1369	7771	4884	2266
90-100	2.6-4.9	(858)	1116	2373	654
	5.0-8.3	(1171)	1325	639	924
	8.4-11.3	(33)	495	236	737
	11.4-14.3	(16)	181	92	269
	Total	(2145)	3377	3718	2794
100-110	2.6-4.9	(858)	3536	(2384)	2722
	5.0-8.3	(1171)	1149	(961)	1138
	8.4-11.3	(33)	297	(363)	434
	11.4-14.3	(16)	33	(111)	88
	Total	(2145)	5115	(3993)	4636
60-110	2.6-4.9	2755	8562	7782	3750
	5.0-8.3	2749	5339	2672	2986
	8.4-11.3	285	1402	1154	1842
	11.4-14.3	136	350	340	533
	Total	6176	16444	12688	9701

Values are x 10^9 larvae; parentheses denote extrapolated values.

In addition to being displaced southward, larvae were farther offshore in 1979 (Table 4). Few larvae were collected offshore of the islands in 1978 (Figures 3-9), and offshore larvae commonly occurred in 1979 (Figures 10-13). The mean distances offshore of larvae for the 4 cruises between January and May (with larval census as weighting factor) were as follows:

	2.6-4.9mm	*5.0-8.3*	*8.4-11.3*	*11.4-14.3*
1978	60 km	56	53	46
1979	85	86	89	117

The trend with size differs between the years; however, the magnitudes of the trends are small unless one includes values for large larvae, which are based on few positive samples.

The temporal distribution of spawning also differed between the years. In 1978, anchovy spawning was moderately low during December and January, increased to a pronounced peak in early March, and decreased to a low level in May; larval abundance was very low by July and August (Table 2). In 1979, spawning was moderately low in January, and increased to a peak in early March. The peak was not as sharp as in 1978, and spawning was sustained at a

TABLE 4

Average Distance Offshore (km) of Anchovy Larvae

	Cruise						
	7712	7801	7803	7804	7805	7807	7808
2.6-4.9 mm	119	65	65	41	44	72	22
5.0 to 8.3	83	61	67	39	48	52	26
8.4 to 11.3	70	39	60	46	57	174	56
11.4 to 14.3	126	41	46	33	74	172	41
	7901	7903	7904	7905			
2.6 to 4.9 mm	111	65	113	54			
5.0 to 8.3	104	89	89	63			
8.4 to 11.3	59	104	104	74			
11.4 to 14.3	41	130	174	91			

moderate level through May (Table 3)[1]. Integrated over January, March, April, and May, anchovy larvae were 1.2 times more abundant in 1979 than in 1978.

To summarize: spawning during 1978 was compressed spatially and temporally relative to 1979. Spawning during 1979 was displaced southward and offshore, and took place later in the year.

An example of the second summarization procedure is presented in Figure 14. The frequency distributions are highly skewed but adequately described by the mean, m, and contagion parameter, k, of the negative binomial distribution. The slopes of the regressions of $\log_e (m)$ on t ranged from 0.23 to 0.15 during December 1977 and the first 4 months of 1978 (Table 5). We will not interpret slopes based on the low and probably sporadic level of spawning during the summer. During the first 5 months of 1979 the slopes ranged from 0.19 to 0.13.

Interpretation of the slopes of the above regressions as mortality rates requires the assumption of a stable age distribution (i.e., continuous and constant production of newly hatched larvae). The March larval abundance peak clearly violates this assumption, so we set up a hypothetical population to examine the extent of bias that may arise. The simulated population had a seasonal spawning cycle approximated by the normal curve, with peak spawning occurring at the end of March. A number of larvae were hatched each day, according to the distribution, and allowed to die at an instantaneous mortality rate of 0.15. Numbers of surviving larvae by age were summarized by month, and the instantaneous mortality was recalculated. Mortality is overestimated when spawning is increasing and underestimated when spawning is declining; the bias increases with seasonal contraction in spawning (Table 6). The bias is asymmetrical, greater when spawning is increasing; however, when larval numbers are accumulated over the entire season, the biases tend to cancel out. The observed seasonal decline in the slope of the larval catch curve (Table 5) is exactly as expected from constant mortality and the observed seasonal changes in larval production.

TABLE 5

Regressions of Larval Production Rates on Age

	Cruise						
	7712	7801	7803	7804	7805	7807	7808
A	4.87+.36	4.39+.18	5.53+.11	4.82+.17	2.87+.30	1.13+.35	3.62+.24
B	0.23+.03	0.16+.01	0.18+.01	0.15+.01	0.11+.02	0.03+.03	0.22+.02
C	.91	.96	.98	.95	.72	.01	.92

		7901	7903	7904	7905		
A		4.23+.26	5.32+.16	5.10+.36	4.82+.16		
B		0.19+.02	0.17+.01	0.19+.02	0.13+.01		
C		.93	.97	.88	.93		

A = ln (m_0)+s.e.
B = z +s.e.
C = r^2

TABLE 6

Estimated Mortality Rates from Age Distributions Pooled over 30 Days When Actual Mortality is Constant at 0.15, and Spawning Follows a Normal Distribution in Time

Std. deviation of spawning curve	Jan.	Feb.	Mar.	Apr.	May	June	Summed over season
30 days	0.24	0.20	0.17	0.14	0.11	0.08	0.15
45	0.22	0.18	0.16	0.15	0.13	0.12	0.15
60	0.21	0.16	0.15	0.15	0.14	0.13	0.15

We calculated an annual estimate of mortality using the larval catch accumulated over each spawning season. The instantaneous mortality of young larvae in 1978—0.175—was not significantly different from that for 1979—0.161.

DISCUSSION

The ultimate importance of events in the larval stage is their effect on survival into the juvenile stage. We have information regarding the between-year and also within-year variation in survival. Differences in larval anchovy survival between 1978 and 1979 may be inferred from the age distribution of the commercial landings of anchovy; despite greater production of larvae in 1979, the 1978 year class was about twice the size of the 1979 year class (J. Sunada, California Department of Fish and Game, pers. comm.). Methot (1981) described the temporal distributions of birthdates of juvenile fish sampled from these 2 year classes. In both years larval abundance peaked in March, and March was the commonest birthmonth (Figure 15). Neither year class was dominated by individuals born during some short period. Thus survivorship within 1978 and 1979 was proportional, for the most part, to larval production. Deviations from constant survivorship may be characterized as greater survivorship of spring 1978 spawn relative to winter 1978 spawn and the reversed seasonal pattern in 1979. This pattern of deviations was not evident in our estimates of early larval mortality. The twofold difference in survival between the years appears to be at least as large as the survival variability within the years.

In discussing the above survival patterns, we must consider the environmental conditions during these 2 years. Winter mixed-layer temperatures were cooler in 1979 than 1978; the Los Angeles Bight temperature ranged from 14° to 15°C in March 1978 and 12° to 13°C in March 1979. The incursion of a cold-water tongue into the Los Angeles Bight was evident in April 1978 and not in April 1979; the southern shift of spawning in 1979 may have been a reaction to thermal conditions or avoidance of an upwelled water mass

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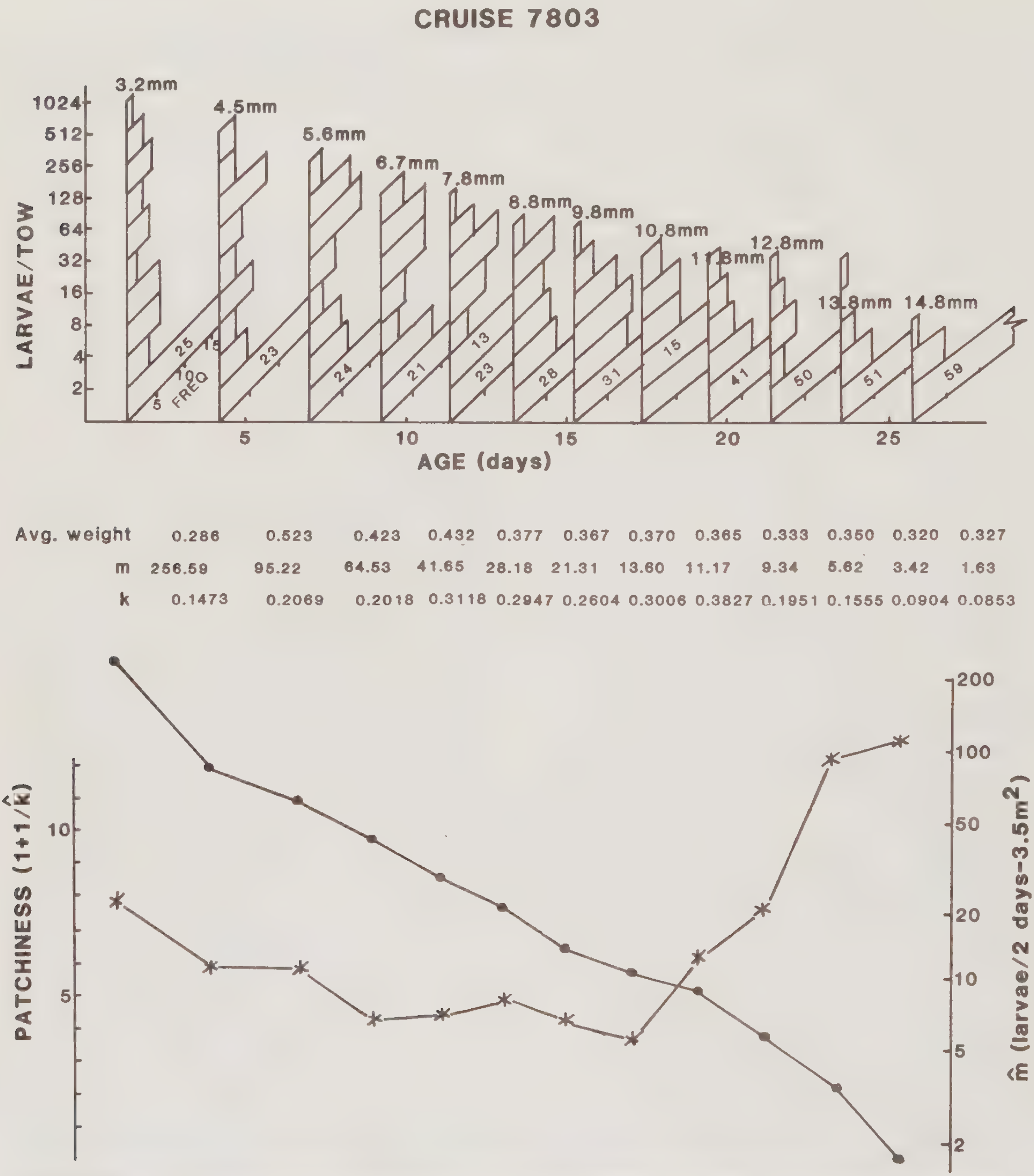
[1] No eggs and a few small larvae were detected during a nonstandard cruise in June 1979 (Methot, unpubl. data).



Avg. weight	0.286	0.523	0.423	0.432	0.377	0.367	0.370	0.365	0.333	0.350	0.320	0.327
m	256.59	95.22	64.53	41.65	28.18	21.31	13.60	11.17	9.34	5.62	3.42	1.63
k	0.1473	0.2069	0.2018	0.3118	0.2947	0.2604	0.3006	0.3827	0.1951	0.1555	0.0904	0.0853

Figure 14. The sample distributions of sized larvae, from cruise 7803, can be approximated by negative binomial distributions defined by the parameters *m* and *k*.

(Lasker et al. 1981). By May of both years, a tongue of cool water extended southeastward off Pt. Conception; pockets of cold water were adjacent to the central California and northern Baja California coasts; and a warm-water plume trailed to the southeast off Santa Catalina Island. There were no obvious differences in

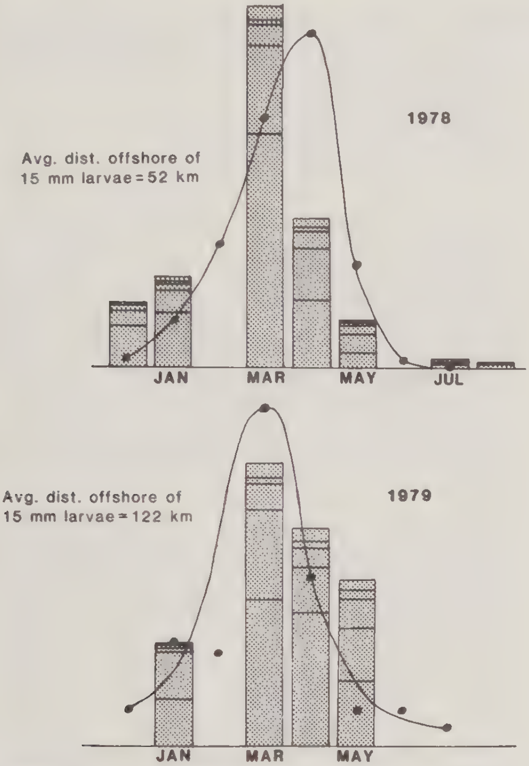


Figure 15. The seasonal distribution of larvae (bars) agreed generally with the birthdate distribution of survivors (line). The height of the bars is proportional to the abundance of larvae; bar subdivisions are proportional to the abundance of four size groups of larvae. The dots represent the fraction of juvenile fish that were spawned in each month.

the May temperature distributions that correlated with the dramatic difference in spawning activity.

Strong storms occurred during the winter of 1978, and substantial stratification of the upper water column was delayed until March 1978. Lasker (1981) suggests that this turbulence prevented formation of prey aggregations considered necessary to anchovy larvae. We did not find increased larval mortality during winter 1978, but Methot (1981) did find that survivorship increased during the 1978 spawning season. However, if larval survival was low during winter 1978 then postlarval survival must have been high throughout 1978 because the 1978 year class was abundant. Also, the winter of 1979 was less stormy, and the 1979 year class was only half as abundant as that from 1978.

Transport of larvae may be responsible for the difference in survivorship between 1978 and 1979. Upwelling and offshore transport of surface water caused by the stress of NW winds were extremely low during winter 1978, and remained below normal through May 1978. Upwelling was again low during winter 1979 but returned to normal by spring. Parrish, Nelson, and Bakun (1981) suggest low upwelling will entrain larvae closer to shore and lead to higher survivorship. Changes in the onshore-offshore distribution of larvae need not affect our estimates of early larval mortality rates. The important affected factor is the fraction of larvae capable of being recruited to the nearshore juvenile habitat. The seasonal pattern of survivorship in 1978 is not consistent with the drift hypothesis, but the seasonal pattern in 1979, the offshore distribution of larvae in 1979, and the relative year-class strengths do support this hypothesis.

We conclude that, in 1978 and 1979, significant variations in survival occurred during the late larval through juvenile stages. We also conclude that there is reason to doubt that larval surveys alone are sufficient to consistently predict recruitment.

In addition to the factors affecting survival of spawn, attention should be addressed to the factors affecting the production of spawn and its distribution in time and space. Since 1966, the central population of the northern anchovy has contracted spatially, expanded the spawning season, exhibited north/south shifts in the spawning center, and varied the month of peak spawning activity from January to May (Hewitt 1980).

ACKNOWLEDGMENTS

The material presented here has been extracted from our Ph.D. dissertations. The work was accomplished with the support and encouragement of our doctoral committees and the Southwest Fisheries Center. We especially wish to thank Drs. Reuben Lasker, John Hunter, and Paul Smith for their advice and critical review.

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HUNTER AND COYNE: ONSET OF SCHOOLING IN NORTHERN ANCHOVY LARVAE
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THE ONSET OF SCHOOLING IN NORTHERN ANCHOVY LARVAE, *ENGRAULIS MORDAX*

JOHN R. HUNTER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

KATHLEEN M. COYNE
Southhampton College
Long Island University
Southhampton, New York 11968

ABSTRACT

Laboratory measurements indicate that schooling begins in larval northern anchovy when they are between 11 and 12 mm standard length and is well established when they reach 13-15 mm. The onset of schooling closely parallels an increase in patchiness of larvae in the sea, and it begins during the period that larvae form a duplex retina and undergo major changes in their respiratory and locomotor systems.

RESUMEN

Observaciones sobre larvas de *Engraulis mordax* en el laboratorio indican que la formación de cardúmenes se inicia cuando las larvas alcanzan de 11 a 12 mm de longitud normalizada, y el cardumen ya está bien definido en larvas de 13 a 15 mm de longitud. La formación del cardumen se produce coincidiendo bastante con el período en que la distribución de las larvas en el mar muestra un incremento en la formación de agrupaciones, y además se inicia cuando la larva adquiere una doble retina y experimenta cambios notables en sus sistemas respiratorio y natatorio.

INTRODUCTION

Except for a portion of the larval stage, all life activities of northern anchovy—feeding, avoiding predators, migrating, and reproducing—are conducted within schools. Thus the time at which schooling begins is an important event in the life history of anchovy, for it identifies the first time that they may be able to profit from schooling. In the larval stage the most important benefit of schooling may be a reduction in predation and cannibalism, although facilitation of the search for food and timing of vertical migration might be additional benefits. For example, fry of the freshwater fish *Gobiomorus dormitor* have a 30 percent chance of being eaten when alone, whereas one individual in a school has a chance of less than 1.5 percent (McKaye et al. 1979). Thus, identifying the larval size at which schooling begins is necessary to properly understand the effects of predation, cannibalism, and food abundance on size-specific mortality rates.

Our objective was to identify the period when schooling begins, by observing the behavior of northern anchovy larvae reared in the laboratory. The ontogeny of schooling behavior has been studied in detail in *Menidia menidia* by Shaw (1960 and 1961) and Williams and Shaw (1971), in *Atherina mochon* by Jorné-Safriel and Shaw (1966) and Williams (1976), and in various cichlids by Dambach (1963). The focus of these past studies was on describing the development of this behavior, the effects of isolation, and the behavioral mechanisms underlying school development. Our focus was more limited, as we wished simply to determine the minimum larval size or age at which schooling might be expected to begin in the sea. Thus larvae were maintained in large communal rearing containers rather than in isolation, and behavioral measurements were designed to identify the onset of schooling but not to understand the underlying behavioral mechanisms.

METHODS

Culture

Three groups of anchovy larvae were reared on a diet of *Gymnodinium splendens*, *Brachionus plicatilis*, and the harpacticoid copepod *Tigriopus californicus*, using methods outlined by Hunter (1976). Eggs were obtained from the induced spawning of fish maintained in the laboratory (Leong 1971). Three thousand eggs were stocked in each of three black fiberglass cylindrical tanks (122 cm diameter, 36 cm deep); the initial water depth was 18 cm (200 l) and increased from daily additions of seawater containing algae and food to about 400 l in about 20 days. Larval density in the three tanks during the time schooling occurred were 3.5 larvae/l (group 1), 1.7 larvae/l (group 2), and 4.3 larvae/l (group 3). In group 3 the water volume of the tank was reduced just before the behavior observations were begun, increasing the density from 2.1 to 4.3 larvae/l. Larvae were not transferred but were observed directly in the rearing tank. Each tank received about 2000 mc at the surface for 12 hours and dark for 12 hours; water temperature was maintained between 15.6 and 16.4°C. Ten or more larvae were sampled every other day to measure growth, and the daily change in schooling behavior was expressed as a function of mean larval length.

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Indices of Schooling Behavior

In active fishes such as the northern anchovy, schooling produces cohesive groups in which the individuals maintain more or less parallel orientation. In some species of schooling fishes, parallel orientation may not be a good index of schooling, but in anchovy it is a natural consequence of their continuous movement and mutual attraction. Thus as schooling develops in larval anchovy, the social attraction among individuals will become stronger, groups or pairs will be more cohesive (remain together for longer periods), individuals will approach one another more often by parallel alignment, and parallel orientation will persist for longer periods. To measure the onset of schooling in larval anchovy we used three indices of these schooling characteristics: frequency of parallel orientation, the cohesion of pairs, and pair cohesion with parallel orientation.

Each morning seven individual larvae were observed for 5 minutes each; another seven were observed in the same manner for 5 minutes each afternoon. Observations were taken at least 2 hours after food was added to the tank. Daily observations began when larvae reached 10-13 mm and ended when the schools became highly reactive to the observer's presence. Interactions of the selected larva with other larvae in the rearing container were recorded with a keyboard and a multiple-pen event recorder. An interaction was defined as an encounter between a selected larva and another larva at a distance of 1 body length or less (a 1-cm grid etched on the bottom of the tank was used to judge distances). The duration of each interaction (seconds the pair remained at 1 body length) was recorded, as was the orientation of the interacting pair. Orientation was classified (Figure 1A) as (a) parallel (aligned side by side or head to tail); (b) head-to-head; and (c) perpendicular (aligned body to head). If the initial encounter were head-to-head or perpendicular, but subsequently one larva followed the other, resulting in parallel alignment, the event was classed as parallel orientation. The frequency of parallel orientation was estimated for each larva by calculating the percentage of all parallel interactions. The cohesion of pairs was estimated by calculating the total time the selected larva was within one body length of any other larva (regardless of orientation) and expressed as a percentage of the total observation time (5 minutes). Pair cohesion with parallel orientation was estimated by calculating the total time the selected larva was parallel to and swam within one body length of any other larva; this was expressed as a percentage of the total observation time. Means for each of these three indices were calculated for each daily set of 14 larval observations.

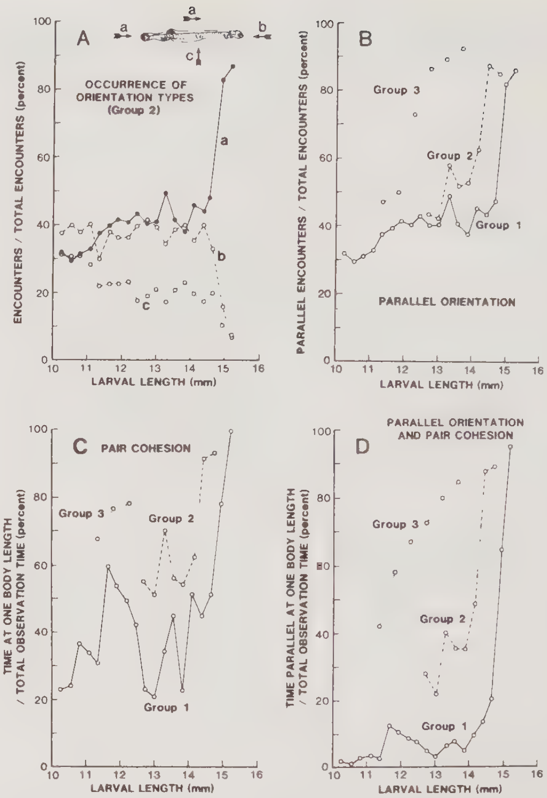

Figure 1. Indices of schooling as a function of the mean length of larval northern anchovy in three rearing containers (groups 1, 2, and 3). Each point is the mean of 14 five-minute behavior observations on different larvae.
A. Percentage occurrence of the three orientation classes during encounters between an observed larva and other larvae in group 2; orientation classes illustrated at top of panel: a, parallel; b, head to head; and c, perpendicular.
B. Percentage of encounters in which parallel orientation occurred in groups 1-3.
C. Percentage of the observation time a larva was within 1 body length of another larva (regardless of orientation).
D. Percentage of the observation time that a larva was aligned parallel to and swimming within one body length of another larva.

RESULTS

Larvae began showing signs of parallel orientation when they reached between 11 and 12 mm standard length. Before this time, when a larva approached another larva head on or perpendicular to the body, one of the pair would dart away in the opposite direction or occasionally would continue in a straight path showing no change in behavior. When larvae reached 11-12 mm a perpendicular approach often resulted in a turn by one of the larvae and a brief period of parallel swimming. Such events were scored as parallel encounters, although the initial approach was not parallel. The frequency of these encounters increased rapidly as the larvae grew (Figure 1 A, B). A sharp increase in the frequency of parallel encounters oc-

TABLE 1
Percentage of Observation Time Larval Northern Anchovy in Groups 1, 2, and 3[1] Were Schooling at Various Ages and Mean Lengths

	Group 1			Group 2			Group 3		
Larval length[3] (mm)	Larval age (days)	Schooling[2] (percent) mean	Schooling[2] (percent) 2XSE[4]	Larval age (days)	Schooling[2] (percent) mean	Schooling[2] (percent) 2XSE[4]	Larval age (days)	Schooling[2] (percent) mean	Schooling[2] (percent) 2XSE[4]
10.3				16	2	1			
.4									
.5				17	1	1			
.6									
.7									
.8				18	3	1			
.9									
11.0									
.1				19	3	1			
.2									
.3							23	42	19
.4				20	3	1			
.5									
.6				21	13	4			
.7									
.8							24	58	29
.9				22	11	3			
12.0									
.1									
.2				23	9	4			
.3							25	67	28
.4									
.5				24	8	3			
.6									
.7	31	28	11	25	5	2	26	72	12
.8									
.9									
13.0	32	22	7	26	3	1			
.1									
.2							27	80	13
.3	33	40	11	27	7	2			
.4									
.5									
.6	34	35	15	28	8	3	28	85	14
.7									
.8				29	5	3			
.9	35	35	14						
14.0									
.1				30	10	2			
.2	36	48	14						
.3				31	14	6			
.4	37	88	14						
.5									
.6									
.7	38	88	15	32	20	7			
.8									
.9				33	65	13			
15.0									
.1									
.2				34	95	4			

[1] Larvae were first observed at age 31d (group 1), 16d (group 2), and 23d (group 3).
[2] Percentage of observation period pairs are at 1 body length and swimming parallel.
[3] From regression of larval standard length on age in each group rounded to the nearest 0.1 mm.
[4] 2 X standard error of the mean where N = 14.

curred between 12 and 14 mm, depending on the laboratory group. By 15 mm all laboratory groups showed a strong schooling response. At this time they also became much more reactive to movements of the observer, although we moved as little as possible.

Within a particular group the three indices of schooling behavior (Figure 1 B, C, and D) showed the same trend with larval length (r^2 values for comparisons between pairs of indices within each of the three experimental groups ranged from 0.72 to 0.99). Thus to document the rest of this presentation we shall use only one index, the percentage of time spent swimming at one body length in parallel orientation (Figure 1 D). This index incorporates both the cohesive and the orientation properties of school structure. We also give the error terms for this index in Table 1, but for clarity they are deleted in Figure 1.

The timing of the onset of schooling varied among the three groups. It was the earliest in group 3 where the index for cohesion with parallel orientation attained values of 80-90 percent at 13.3 mm (age 27 days). Comparable values for group 1 occurred at 14.4 mm (age 37 days) and in group 2 at 15.2 mm (age 34 days).

Thus schooling had become clearly established in anchovy larvae by the time they attained a length of 13 to 15 mm. In other words, 13-15-mm larvae swam parallel to their neighbors at about a body length apart for 80-90 percent of the observation time. In group 3 the water in the tank was reduced by one-half when the larvae averaged 11.4 mm. After this disturbance the larvae immediately began to show signs of schooling, and they formed a relatively uniform school by 12.5 mm. It is not known if the increase in larval density (by a factor of 2) caused the early onset of schooling in group 3. The timing of the onset of schooling in the other two larval groups displayed a reverse pattern with larval density. We are more inclined to believe that the disturbance of changing the water and the resulting fright response induced an early onset of schooling. Examination of Figure 1 D or Table 1 indicates that the rate of change was more rapid in groups 1 and 2, where the onset of schooling began at somewhat longer length. This may indicate that the capability for schooling develops between 11 and 12 mm, but that external stimuli, perhaps a fright response, trigger the behavior. Schooling was not obvious in any group until 1 to 1½ hours after feeding, and if food

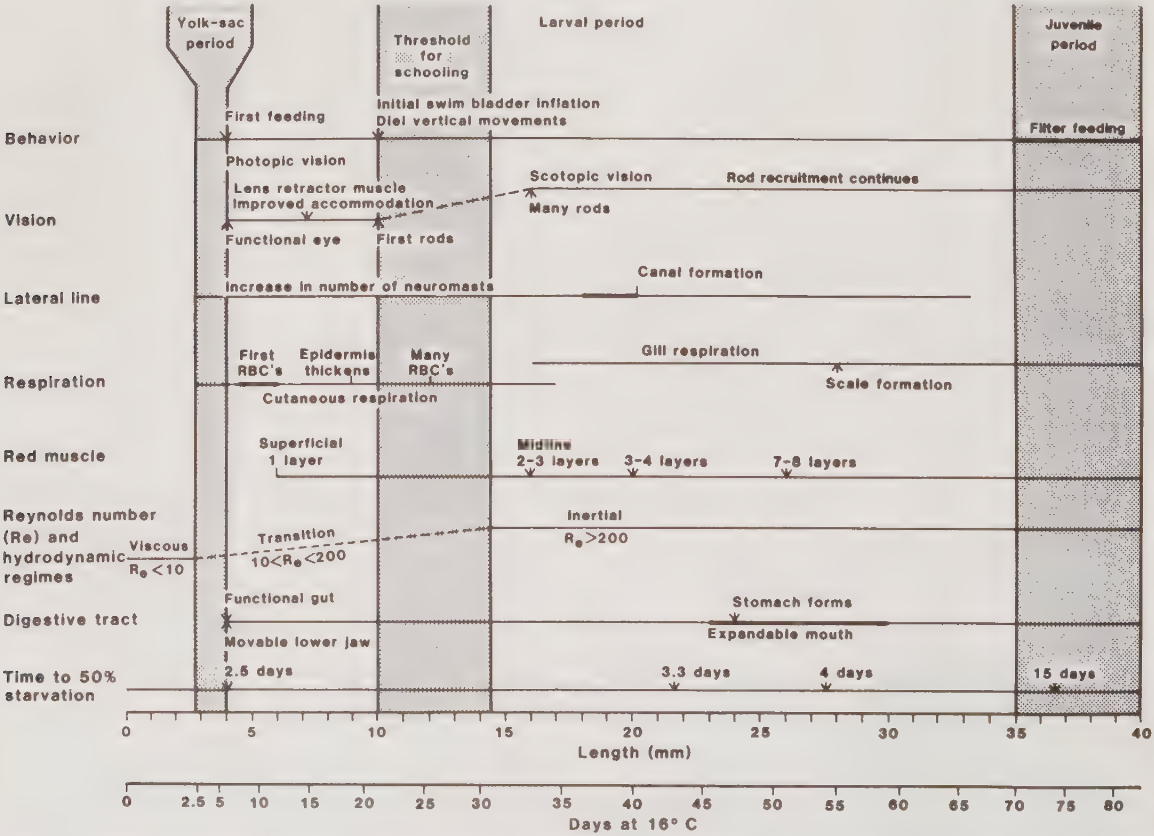
Yolk-sac period
Threshold for schooling
Larval period
Juvenile period
Behavior
First feeding
Initial swim bladder inflation
Diel vertical movements
Filter feeding
Vision
Photopic vision
Lens retractor muscle
Improved accommodation
Functional eye
First rods
Scotopic vision
Many rods
Rod recruitment continues
Lateral line
Increase in number of neuromasts
Canal formation
Respiration
First RBC's
Epidermis thickens
Many RBC's
Cutaneous respiration
Gill respiration
Scale formation
Red muscle
Superficial 1 layer
Midline 2-3 layers
3-4 layers
7-8 layers
Reynolds number (Re) and hydrodynamic regimes
Viscous $R_e<10$
Transition $10<R_e<200$
Inertial $R_e>200$
Digestive tract
Functional gut
Movable lower jaw
Stomach forms
Expandable mouth
Time to 50% starvation
2.5 days
3.3 days
4 days
15 days
0
5
10
15
20
25
30
35
40
Length (mm)
0
2.5
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
Days at 16° C

Figure 2. The timing of the onset of schooling in relation to events in the maturation of northern anchovy larvae. Structural events are from O'Connell (1981); hydrodynamic events from Weihs (1980); and all others from Hunter (1976), and Hunter unpublished data.
RBC = red blood cells. Time to 50 percent starvation is number of days of starvation at which 50 percent of the fish died.

was insufficient the larvae appeared not to school. All data presented here were taken at least 2 hours after feeding on an abundant supply of food.

DISCUSSION

The size of anchovy larvae at the onset of schooling is about the same as that determined for the marine silversides *Menidia*. Schooling (swimming continuously as a group) in *Menidia* is clearly established when they reach 10-12 mm (about 20 days old) (Shaw 1960; Williams and Shaw 1971). The period in larval development at which schooling begins is probably partially a function of the maturation rates of organ systems. Anchovy of this size (12-15 mm) are characterized by rapid structural and behavioral changes (Figure 2). At 7 mm, shortly before the onset of schooling, the lens retractor muscle becomes functional, increasing visual accommodation (O'Connell 1981). At 10 mm the swim bladder is inflated for the first time at the water surface; larvae begin nightly migrations to the water surface (Hunter and Sanchez 1976); and the first rods appear in the retina. Over the interval in which schooling begins (12-15 mm) the number of rods increases, perhaps improving peripheral vision; the red muscle deepens from a superficial layer to 2-3 layers deep; and the larva changes from a cutaneous respirator to a gill respirator (O'Connell 1981). In addition, by the time they reach 15 mm larvae have passed a transitory hydrodynamic regime where water viscosity has an important effect on swimming performance, and entered one in which performance is independent of viscosity effects, thus permitting maximum efficiency in the beat-and-glide swimming characteristic of anchovy (Weihs 1980). All organ systems continue maturing throughout the larval phase, but the above circumstantial evidence indicates that onset may be tied to changes related to locomotor efficiency (metabolism and swimming kinetics) and improvements in the visual system.

Although structural developments may set the stage for the onset of schooling, the actual initiation may be triggered by environmental events. In the laboratory, schooling seemed to be triggered by various disturbances such as changing the tank water, cleaning the tank, or other fright-inducing stimuli. In the sea the appearance of predators or perhaps initiation of diel vertical movements to the sea surface could be triggering mechanisms. Such disturbances could act as a trigger only after the larvae reach the appropriate age for onset of schooling.

Hewitt (1981a and b) measured the mean patchiness of the eggs and larvae of northern anchovy taken in ichthyoplankton surveys over the years 1951-79 (6,000+ samples) using Lloyd's (1967) index of patchiness. He showed that initially anchovy eggs are quite patchy in the sea, as could be expected from the schooling habits of the parents. After spawning, however, a gradual process of dispersion begins; eggs and, subsequently, larvae become more and more dispersed until the larvae reach about 10 mm (20 days old), whereupon this trend is reversed, and larvae become increasingly more patchy with larval size or age. We have reproduced Hewitt's (1981b) data and plotted on Figure 3 the average schooling index for the data given in Table 1. The increase in patchiness with larval length in the sea closely matches the onset of schooling averaged for the three groups. Thus as Hewitt (1981a) suggested, the change in patchiness—a statistical property of the spatial distribution of larvae—is an effective measure of the onset of schooling in the sea.

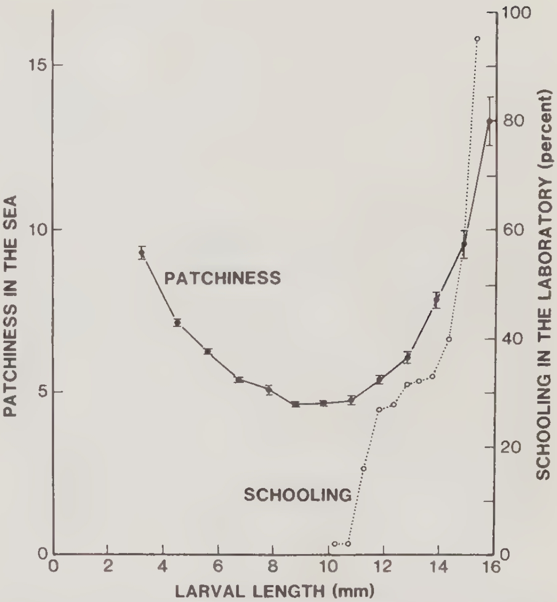

Figure 3. Patchiness of larval anchovy in the sea as a function of larval length (from Hewitt 1981b) and the onset of schooling in the laboratory. Patchiness (solid line), measured by Lloyd's (1967) index, is a measure of the degree of departure of larval spatial distributions in the sea from random dispersion; bars are two standard errors for the index of patchiness. The onset of schooling in the laboratory (dotted line) is measured by the mean percentage of the observation time that larvae were parallel and swimming one body length apart; points are the mean for three laboratory groups combined by length classes.

A salient feature of larval anchovy schools in the laboratory was that they were dispersed before the daily additions of food, and schooling was not obvious until the larvae had fed. Schools of juvenile jack mackerel also are less cohesive before feeding (Hunter 1966). The restriction of our measurements to post-feeding groups was appropriate for a threshold estimation, but it did mask the fact that the time spent in organized cohesive schools increases throughout the anchovy's larval and juvenile periods (van Olst and Hunter 1970). This gradual increase in the time spent in schools may be related to the maturation of the digestive and feeding systems, which occurs in the juvenile period. Maturation of the digestive system, onset of satiation mechanisms, increases in body reserves, and increases in feeding efficiency probably reduce the time required for feeding and food search and consequently permit schooling to continue for longer periods each day. For example, northern anchovy larvae < 10 mm feed throughout the day and do not appear to satiate. On the other hand, adults satiate rapidly when they feed by biting large prey, and consume a full ration in less than an hour. Satiation is not evident when they feed by filtering smaller prey, but this behavior causes little disruption of school organization, whereas biting behavior affects school structure (Leong and O'Connell 1969).

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THRESHOLDS FOR FILTER FEEDING IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

JOHN R. HUNTER AND HAROLD DORR
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

The density threshold for the onset of filter feeding in adult anchovy *(Engraulis mordax)* fell between 5 and 18 *Artemia salina* nauplii/l, between 1 and 2 anchovy eggs/l, and between 151 and 328 *Gymnodinium splendens* cells/l. Observations of the incidence of filtering schools indicate that behavioral changes occurred at lower food densities. These observations also indicate that the intensity of filtering by anchovy schools may be a function of the biomass of filterable foods. Filtering persisted long after the density in the tank was reduced below that required for the initiation of filter feeding.

RESUMEN

La densidad mínima para el comienzo de alimentación por filtrado en adultos de *Engraulis mordax* disminuyó entre 5 y 18 nauplios de *Artemia salina* por litro, entre 1 y 2 huevos de anchoveta por litro, y entre 151 y 328 células de *Gymnodinium splendens* por litro. Observaciones sobre la incidencia de cardúmenes en proceso de actividad filtradora indican que se producen cambios en su comportamiento cuando el alimento aparece en densidades bajas. Estas observaciones también indican que la intensidad de filtrado en los cardúmenes de anchoveta puede estar determinada por la biomasa de alimento filtrable. Este tipo de alimentación aún persistió mucho después de que disminuyera la densidad en el tanque, alcanzando valores por debajo del umbral que marca el comienzo del proceso de alimentación por filtrado.

INTRODUCTION

Northern anchovy are facultative filter-feeding planktivores. They change from filter feeding to particulate feeding on the basis of prey size; they filter small prey, such as *Artemia salina* nauplii, and bite larger ones, such as *Artemia* adults (Leong and O'Connell 1969). A significant proportion of the natural mortality of northern anchovy eggs can be attributed to adult anchovy filtering their eggs (Hunter and Kimbrell 1980; MacCall 1980), but the extent to which eggs are filtered selectively or taken inadvertently while filtering other prey is not known. Selective filtering requires that the density of prey be sufficient to cause the school to filter intensively within an aggregation of a particular prey. Thus, the prey density thresholds for filter feeding are important in modeling effects of egg cannibalism as well as in understanding the ecology of anchovy feeding. The densities of prey used by Leong and O'Connell (1969) to estimate maximum filtering rates of anchovy (292-1,120 *Artemia* nauplii/l) are far above the threshold. The objective of this study was to estimate the prey density threshold for filtering in northern anchovy. Three prey types are used: *Artemia* nauplii (0.433 mm x 0.236 mm; 1.70 μg dry weight); northern anchovy eggs (1.34 mm x 0.66 mm; 30.1 μg dry weight); and the dinoflagellate *Gymnodinium splendens* (40 μm dia; 0.0117 μg dry weight).

METHODS

Schools of 56-596 northern anchovy (6.4-10.2 cm standard length) were maintained in a tank (3-m dia.; water depth 0.6 m) with continuous flowing seawater of ambient temperature (14.3-21.6°C). Seawater was filtered continuously through a sand-and-gravel filter and subsequently was irradiated with ultraviolet light. The tank was dimly lit from above by a 40-W incandescent lamp for 12 h per day and was dark for 12 h. Fish were fed trout food (Oregon Moist Pellets)[1] and frozen adult *Artemia salina* (brine shrimp). Schools were deprived of food for 48 h prior to an experiment, and a few hours before a test the tank was cleaned and the seawater shut off. Numbers of anchovy in schools varied (Table 1), and the tank was completely restocked 11 times over the 2 years that experiments were conducted. Partial restocking and some mortality account for the variability in school size.

At the onset of an experiment the tank was stirred vigorously with a large dip net (60-cm dia); the school recovered from this disturbance in 1-2 min. Immediately after stirring, the incidence of filtering behavior was recorded for 9 min. Food was then added and the tank stirred again while water samples were taken to estimate the density of food in the tank. After the tank was stirred for the second time, behavior ob-

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[1] Use of a trade name does not imply endorsement by the National Marine Fisheries Service.

TABLE 1

Effect of Prey Density and Prey Type on Filter Feeding in Northern Anchovy, *Engraulis mordax*, Schools

Food type			Incidence of filter feeding			
Initial density n/l	Final[1] density n/l	Significance of density change[2]	Before food added[3]	After food added[3]	Significance of change[4]	School Size n
Artemia nauplii						
0.87	0.76	0	0	1.2	0	430
2.81	2.84	0	7.6	7.9	0	430
3.27	2.22	0	0.6	4.3	+	357
4.59	4.46	0	2.0	3.9	0	300
5.51	2.59	+	14.5	43.7	+	318
5.96	1.68	+	3.3	12.0	+	256
6.71	4.33	0	1.2	7.0	0	300
8.77	8.47	0	0.2	20.0	+	567
9.03	4.60	0	1.6	10.4	+	567
9.13	6.90	0	0.1	0.3	0	357
13.10	11.40	0	1.6	5.4	+	357
13.62	9.62	+	2.1	26.8	+	318
16.05	10.14	0	0	25.5	+	357
18.04	8.74	+	12.6	36.1	+	430
18.79	10.71	+	3.6	49.7	+	300
20.46	9.44	+	2.1	57.4	+	430
23.96	9.17	+	8.6	47.5	+	430
26.64	12.85	+	10.8	70.7	+	430
114	—	—	—	57.8	—	438
190	—	—	—	53.4	—	569
285	—	—	—	86.0	—	596
378	—	—	—	71.9	—	167
386	—	—	—	81.8	—	374
Anchovy eggs						
0.26	0.15	0	3.9	20.5	+	106
0.32	0.37	0	0.2	7.6	+	75
1.11	1.52	0	1.8	22.7	+	300
1.50	0.46	+	4.1	59.5	+	116
3.32	1.70	+	2.1	45.8	+	131
4.14	1.21	+	5.0	63.2	+	357
4.76	0.84	+	3.9	80.1	+	300
5.34	0.73	+	5.1	58.6	+	256
10.50	2.90	+	1.6	79.8	+	126
Gymnodinium cells						
151	104	+	0.2	7.8	+	—
161	104	0	2.1	31.2	+	—
259	200	+	0.4	9.3	+	56
328	358	0	0.6	3.2	+	67

[1] Measured 9 min after food introduction in *Artemia* and egg experiments, and after 18 min in *Gymnodinium* experiments; five highest *Artemia* densities were preliminary experiments, and no final density was recorded.

[2] Comparison of initial and final density using t-test; + = $P < 0.05$ and 0 = $P > 0.05$ (2 tail).

[3] Average for 9-min test period.

[4] Comparison of mean incidence of filtering before and after food added using t-test when + = $P < 0.05$ and 0 = $P < 0.05$ (2 tail).

servations were resumed for 9 min, then the tank was stirred for the third time while another set of water samples was taken. In the *Gymnodinium* experiments the final set of water samples was not taken until 18 min after the introduction of food, in order to increase the probability of detecting a change in food density, since the filtering response was weak even at the highest density.

Methods for estimating food density in the tank varied. When the density was about four prey per liter or less we took seven 12-liter samples; at higher densities we took 12-15 one-liter samples. Water in each sample was filtered, prey were counted, and a mean density was calculated. The t-test (2 tail) was used to compare initial to final food densities.

Filtering behavior was recorded by three to five observers stationed around the tank. Each observer watched a single anchovy for 2 sec. If the operculum was fully extended during any part of the 2-sec period, the observer recorded a filtering act. After recording on push-button counters whether or not a filtering act had occurred, the observer randomly selected another fish and continued to accumulate 2-sec observations of individual fish over a 2-min period. After 2 min each observer had accumulated a set of about 60 observations of 60 fish; the proportion of these observations in which filtering occurred was transcribed and another 2-min observation period begun. In the 9-min test period, each observer made four sets of cumulative observations, and the number of sets per test period ranged from 12 to 20, depending on the number of observers. Each set was considered as an estimate of the incidence of filtering behavior in the school. The sets taken by all observers during a test period were combined, and a mean and variance were estimated assuming each set to be an independent observation. We used the t-test (2 tail) to determine if sets of observations taken before and after the addition of food differed from each other.

RESULTS

The density threshold for the onset of filtering of *Artemia* nauplii fell between 5 and 18 nauplii/l when a significant difference ($P<0.05$) between initial and final density was the criterion (Table 1). No significant changes occurred at densities less than 5 nauplii/l, and initial and final densities were consistently different above 17 nauplii/1. Significant changes in the density of anchovy eggs occurred consistently at densities greater than two eggs/l, indicating that the threshold for the onset of filtering may occur between 1 and 2 eggs/l. The density of *Gymnodinium* changed significantly in two of the four experiments, indicating that a 50 percent threshold for filtering this dinoflagellate may fall between 151 and 328 cells/l.

Even when no food has been present for some time, usually a few fish, typically about 2 percent, execute filtering movements. The frequency of such acts is low and their duration short: they may serve in early detection of food or may have some other function. At high food densities, similar to those used by Leong and O'Connell (1969), nearly all fish in a school filter, and filtering bouts are nearly continuous. At such densities, about 70-80 percent of the fish filter during any 2-sec period. At lower food densities, the frequency of filtering bouts and their duration decreases, and the time between bouts increases until, at the lowest densities, the behavior approaches that of fish without food.

The percentage of fish filtering usually increased when food was added, even at the lowest densities. Thus, significant changes in filtering behavior occurred at lower densities than those at which we were able to detect a change in food concentration caused by filtering (Table 1). The proportion of fish filtering increased with the initial food density but differed among food types (Figure 1). For a given density, the incidence of filtering was highest for anchovy eggs and intermediate for *Artemia* nauplii; only a small portion of the fish filtered *Gymnodinium* at densities as high as 328 cells/l. A strong response (filtering fish >50 percent) occurred at food densities of 4 eggs/l and 20 *Artemia* nauplii/l; above these densities the incidence of filtering increased gradually with food density, reaching a maximum of about 80 percent.

The behavior data shown in Figure 1 were combined by expressing the initial food density in terms of dry weight per liter instead of numbers per liter. Con-

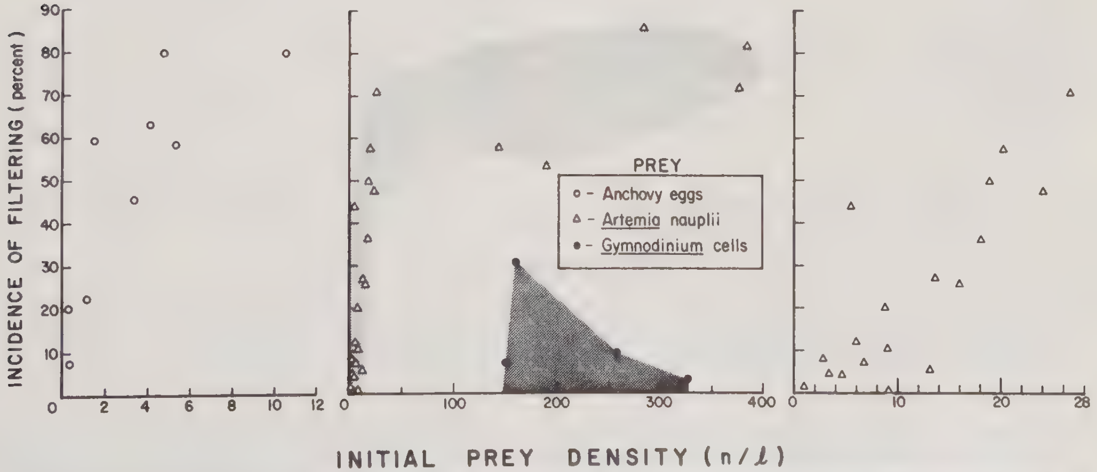

Figure 1. Mean incidence of filter feeding in northern anchovy schools during initial 9 min of feeding as a function of initial prey density in numbers per liter. *Left,* filtering incidence as a function of anchovy egg density; *center,* filtering incidence as a function of density of *Artemia* nauplii (lightly shaded) and *Gymnodinium* cells (darkly shaded); *right,* enlargement of *Artemia* nauplii data for densities of 1-27/1.

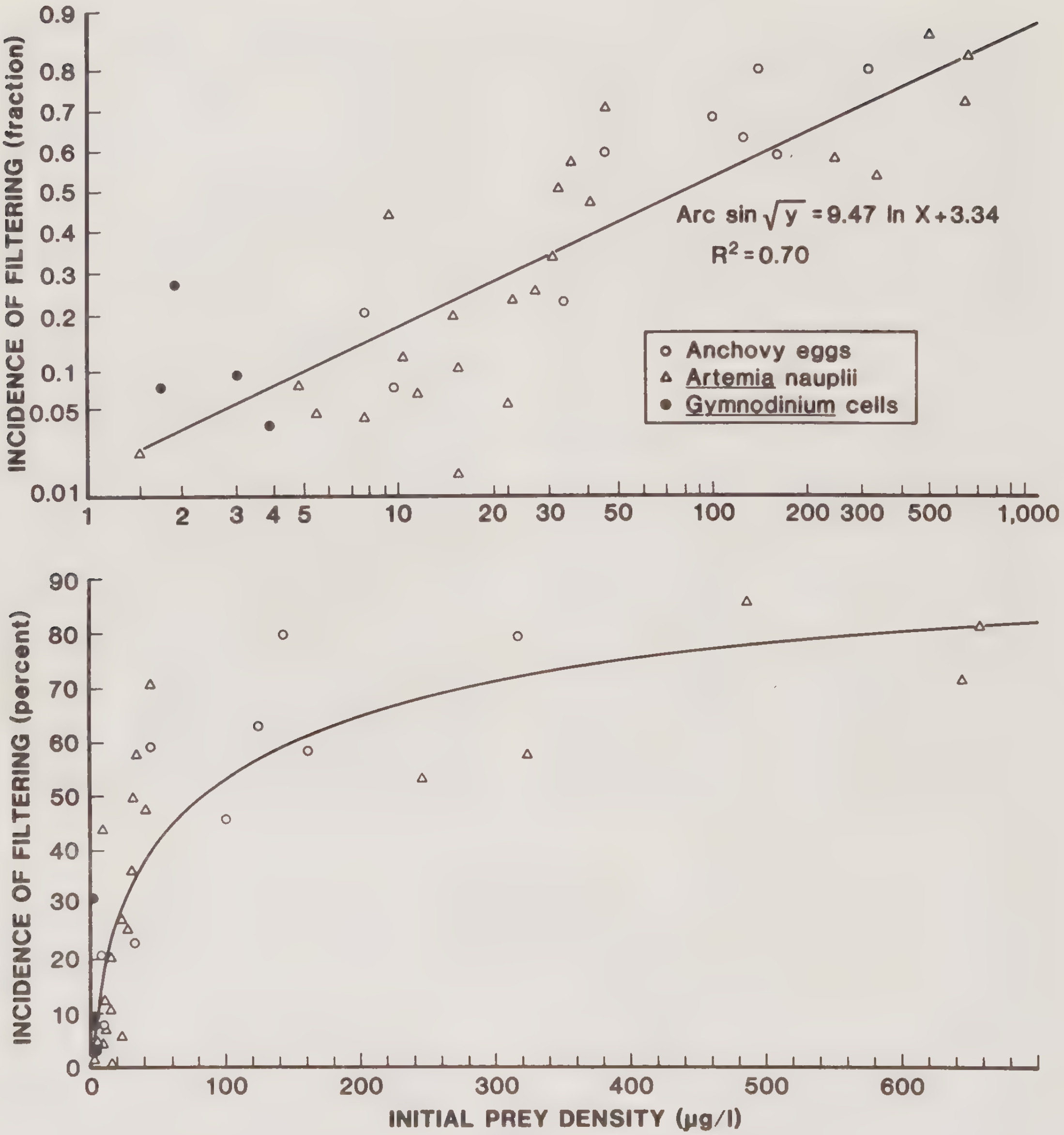

Figure 2. Mean incidence of filter feeding in northern anchovy schools during initial 9 min of feeding as a function of initial prey density in dry weight per liter. Data in Figure 1 have been converted from numbers per liter to dry weight per liter using the conversions, anchovy egg = 30.1 µg; *Artemia* nauplius = 1.70 µg; and *Gymnodinium* cell = 0.0117 µg. *Upper panel*, incidence of filter feeding plotted on arcsine transformed scale (arcsin $\sqrt{y}$) and dry weight per liter on $\log_e$ scale; *lower panel*, both parameters plotted on arithmetic scales, line from equation in upper panel.

version to dry weight brought together the behavior observations made on the three foods even though they were taken at widely different particle densities (Figure 2, upper panel). Because many of the percentages of fish filtering were near the extremes (<30 percent or >70 percent), we used the arcsine transformation of the fraction of fish filtering (Sokal and Rohlf 1969) and regressed the transformed fractions on the $\log_e$ dry weight of prey per liter. The form of the relation between incidence of filtering and dry weight of food per liter (Figure 2, lower panel), resembles the type II predator response of Holling (1965), i.e., a negatively accelerated rise to a plateau. Because of variability in our data, we cannot distinguish statistically between a type II and a type I predator response, which is characterized by a linear rise to a plateau.

The intensity of filtering in anchovy schools may be a function of the density of filterable biomass. Figure 2 indicates that similar responses to different foods occurred at the same density of biomass but not at the same particle density. Because we used only three foods, the results could also be attributed to specific food preferences, the prey weight proportionality being chance. On the other hand, *Artemia* might be expected to be the preferred prey because *Artemia* adults were a routine part of the laboratory diet, but the school responded much more strongly to eggs than to *Artemia* at low prey densities. We conclude that the density of biomass, regardless of prey type, is probably an important factor regulating the intensity of filter feeding in anchovy schools.

In contrast, the lowest concentrations of prey that stimulated filter feeding were inversely related to particle size or mass. A higher concentration of biomass per liter was required to elicit filtering of anchovy eggs than of *Artemia* nauplii, and a higher concentration of biomass was required to stimulate filtering of *Artemia* nauplii than was required for the much smaller particle *Gymnodinium* (Table 2). Threshold prey concentrations for initiating filter feeding are also inversely related to particle size in menhaden (Durbin and Durbin 1975). Thus the intensity of filtering by anchovy schools was proportional to the density of biomass in the water, whereas the threshold concentrations required to initiate filtering were inversely related to biomass. These findings may be explained in the following way. A higher concentration of biomass may be required for initiation of egg filtration than for filtration of *Gymnodinium* cells because at lower egg concentrations it is probably more efficient to bite rather than to filter eggs, whereas it is never efficient to bite an individual *Gymnodinium* cell. In other words, the threshold density for initiation of filtering a particular prey may be a function of the cost of filtering relative to biting the prey, as well as of its mass; this would elevate the filtration threshold for larger filterable prey such as anchovy eggs, which may be profitably eaten either way.

TABLE 2

Density Threshold Range for the Onset of Filter Feeding in Northern Anchovy

	Particle size		Threshold for onset filter feeding	
Food type	Dimensions µm	Dry weight µg	No/l	Dry wt (µg)/l
Anchovy eggs	1340 x 660	30.1	1-2	30-60
Artemia nauplii	433 x 236	1.7	5-18	8.5-31
Gymnodinium	40 x 40	.0117	151-328	1.8-3.8

In five preliminary experiments anchovy schools were given a high initial density of *Artemia* nauplii (29-322 nauplii/l), and the school was permitted to graze the food to low levels over an extended period. The incidence of filtering and the density of *Artemia* nauplii were recorded at intervals over the feeding period. In these experiments filtering activity remained at a high level even when the density in the tank was reduced below that required for the initiation of feeding. The average incidence of filtering at the end of the feeding period was 32 percent, by which time the density of *Artemia* had dropped to an average of 2 nauplii/l (Table 3). In contrast, the incidence of filtering was close to zero when nauplii at densities of 2-4/l were initially offered (see Figure 1, right panel). We observed the same behavior in anchovy that were fed eggs. The tendency for high levels of filtering to persist after nearly all food has been removed seems to be a common characteristic in filter-feeding clupeoids, for similar behavior has been observed in Atlantic menhaden (Durbin and Durbin 1975). Thus, anchovy schools that encounter a dense patch of prey may reduce the density below the threshold for initiation of feeding and consequently have a greater impact on the prey than indicated by filter-feeding thresholds.

DISCUSSION

A strong filtering response to eggs occurred at densities above five eggs/l, and the threshold for the onset of filtering (based on a detectable change in egg density) was between 1 and 2 eggs/l. The density of anchovy eggs in the sea, estimated from horizontal

TABLE 3

Persistence of High Levels of Filtering of Northern Anchovy Schools Fed on Initially High Food Density

Initial density *Artemia* nauplii (n/l)	Initial incidence of filtering[1] (percent)	Duration of feeding (min)	Final density *Artemia* nauplii (n/l)	Final incidence of filtering[2] (percent)	School size (numbers of fish)
322	89	29	3.1	33	488
58	31	27	1.3	42	424
53	57	29	1.4	30	418
39	35	30	3.8	29	486
29	30	28	0.6	27	498
Mean 100	48	29	2.0	32	463

[1] Measured over initial 9 min of feeding.

[2] Measured over last 2 min of experiment.

plankton tows, is typically two or more orders of magnitude below this filtering threshold. On the other hand, very high egg densities are occasionally recorded. The highest density of anchovy eggs taken in a neuston net was 31/1, corresponding to a density of 46,000 eggs/10 m^2 of sea surface, which compares with the upper 5 percent of all anchovy egg samples (ranked by density) taken in oblique tows (nylon nets) by the California Cooperative Oceanic Fisheries Investigations ichthyoplankton surveys (unpublished data Southwest Fisheries Center, La Jolla, California).

The integrating characteristic of plankton tows doubtless underestimates to some extent the peak densities of anchovy eggs actually encountered by an anchovy school. Further, the threshold based on density changes in our tank probably underestimates possible effects, because behavior observations indicated that at least some of the fish are stimulated to filter eggs at densities as low as 0.26 eggs/l. Finally, that as many as 730 eggs have been taken from a single anchovy stomach indicates that at times eggs are highly concentrated in the sea (Hunter and Kimbrell 1980). All of these factors point to the conclusion that at least occasionally anchovy egg densities are sufficiently high in the sea to stimulate filter feeding directly, but that eggs are probably also taken when fish are stimulated to filter by concentrations of other prey. It will require more accurate measurements of egg density in the sea to determine the extent of selective feeding on eggs.

Measurement of the size structure of zooplankton assemblages in front of and behind northern anchovy schools indicates that anchovy feed selectively by consuming relatively more of the larger prey and less of the smaller ones in an assemblage (Koslow 1981). The size of zooplankters selected by anchovy in Koslow's study were frequently less than 1 mm. Adult northern anchovy filter eggs (ca. 1.3 mm x 0.6 mm) and smaller particles, whereas they bite anchovy larvae in the yolk-sac stage (ca. 2.8-4.0 mm) and *Artemia* adults (5-10 mm); (Leong and O'Connell 1969). Since the transition from filtering to biting probably occurs at a prey size between 1 and 3 mm, Koslow's data indicate that selectivity results from filter feeding as well as biting.

At least three mechanisms could cause selectivity in filter feeding: selective ingestion, selective gaping, and selective orientation. Selective ingestion, retention on the gill rakers, and ingestion of a preferred prey might occur, but no evidence exists. On the other hand, the fineness and structure of the gill rakers establishes the minimum size of filterable prey; in a limited sense this could be considered selectivity.

Selective gaping was documented in this paper. Our experiments indicated that the frequency or duration of filtering acts increased with the density of biomass (our behavioral observation methods do not distinguish between increases in frequency or duration of filtering acts, but they appear to covary). Thus, preferred prey can be selected by varying the intensity of filtration, and preferences appear to exist for large filterable prey or for smaller ones at an equivalent density of biomass. In addition, filtering persisted long after the density of prey was reduced to subthreshold levels. This factor amplifies the effect of selective gaping.

Selective orientation of a school to patches of prey can also cause selectivity in filter feeding. When food (*Artemia* nauplii or anchovy eggs) was added to a small area in our test tank the anchovy would interrupt their circuit of the tank when they encountered the patch; at first the school would be disorganized, with individuals independently swimming rapidly in small elliptical orbits while filtering intensively in the area of the food patch. Soon this behavior would become synchronized, with the entire school swimming in a larger elliptical orbit through the food patch while continually filtering. Chemical stimuli alone are sufficient to elicit the first stages of this behavior (change in school direction with individuals swimming independently in small elliptical orbits), but filtering and formation of a well-organized school in the patch require the presence of food (C. Barnett, pers. comm.). Thus, food preferences based on chemical stimuli may cause changes in the direction of school movement that could lead to selective filter feeding.

In conclusion, northern anchovy schools may regulate filtering intensity in accordance with the concentration of filterable biomass in the water, and this probably results in selection of the larger prey in an assemblage. Selectivity also may be accomplished by the school's orientation to chemicals produced by a patch of prey. Since anchovy eggs are large relative to many planktonic foods and occur in dense patches, selective gaping and orientation probably occur. It would be of interest, in this regard, to determine if the intensity of filtering depends upon the largest and most abundant component in an assemblage or on the combined total of all filterable organisms.

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HUSBY AND NELSON: TURBULENCE AND VERTICAL STABILITY IN THE CALIFORNIA CURRENT
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TURBULENCE AND VERTICAL STABILITY IN THE CALIFORNIA CURRENT

DAVID M. HUSBY AND CRAIG S. NELSON
Pacific Environmental Group
Southwest Fisheries Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
P.O. Box 831
Monterey, California 93942

ABSTRACT

Summaries of historical surface marine wind observations and subsurface temperature data are used to examine the seasonal and spatial characteristics of wind-generated turbulent energy production and of stability of the upper water column over the California Current region. A recent hypothesis suggests that survival of first-feeding larval anchovies, *Engraulis mordax*, depends on the aggregation of properly sized food organisms in a stable water column in the absence of strong wind-induced turbulence. A comparison of wind mixing and stability indices for regions encompassing the principal spawning grounds of the three subpopulations of northern anchovy demonstrates that peak spawning occurs during seasons and in locations associated with stable stratification, relatively low rates of turbulent energy production, and weak offshore transport (upwelling).

The average intensity of wind-generated turbulent energy production is similar during peak spawning periods in all three regions. This suggests optimum levels of turbulence and stability in the upper water column—levels that favor survival of first-feeding larvae. Although examination of mean conditions is useful in a comparative study, the average intensity of turbulent wind mixing over a spawning season is not likely to be well correlated with interannual variability in recruitment. Rather, the existence of sufficient time-space windows within which turbulence does not exceed critical values may be the relevant factor. To investigate this possibility, time series of wind-generated turbulent energy production are presented for recent periods associated with large variations in year-class strength.

RESUMEN

Para estudiar las características estacionales y espaciales de la producción de energía eólica turbulenta y la estabilidad de la columna superior de agua en la región de la Corriente de California, se emplean observaciones del viento en la superficie del mar y de temperatura subsuperficial. Ultimamente se ha planteado una hipótesis que propone que la supervivencia de las larvas de anchoveta, *Engraulis mordax*, al iniciar su alimentación, depende del conjunto de organismos alimenticios de medida apropiada presentes en una columna de agua estable donde no existe fuerte turbulencia eólica. Una comparación de los índices de mezcla eólica y los de estabilidad de las regiones que abarcan las principales áreas de desove de las tres subpoblaciones de anchoveta del norte, muestra que el período de máximo desove ocurre en estaciones y lugares en donde la estratificación es estable, los índices de producción de energía eólica turbulenta son relativamente bajos, y la surgencia de aguas es débil.

La intensidad media de la producción de energía eólica turbulenta es igual en las tres regiones durante los períodos de máximo desove. Esto implica que existen niveles óptimos de turbulencia y estabilidad en la parte superior de la columna de agua, los cuales son propicios para la supervivencia de las larvas. Si bien un examen de las condiciones medias es útil en un estudio comparativo y es improbable que la intensidad media de la mezcla eólica turbulenta durante la estación de desove esté bien correlacionada con la variabilidad interanual en el reclutamiento. Más bien parece que el factor determinante podría ser la existencia de suficientes intervalos de tiempo y espacio, donde la turbulencia no excede valores críticos. Para investigar esta posibilidad se presentan series de tiempo de la producción de energía eólica turbulenta de etapas recientes vinculadas con importantes variaciones en la cantidad de anchoveta para cada generación.

INTRODUCTION

The concept of a "critical period" in the early life history of fishes was formulated in Hjort's pioneering studies (1914, 1926) on the year-class strength of Norwegian herring and cod stocks. The critical-period hypothesis suggests that survival of larval fish might be affected by (1) a lack of food at the time of first feeding, and (2) currents that transport larvae to areas unfavorable to further growth. The relationships of nonseasonal fluctuations in surface transport to larval survival and year-class strength have been investigated in recent correlative studies on Pacific mackerel, *Scomber japonicus*, (Parrish and MacCall 1978) and Atlantic menhaden, *Brevoortia tyrannus*, (Nelson et al. 1977). Parrish et al. (1981) have discussed the

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general relationship of surface transport mechanisms to reproductive success of pelagic fishes in the California Current system. However, even where apparent linkages between surface drift conditions and stock variations have been demonstrated, larval survival is still critically dependent on food availability. Hjort emphasized the first of these two critical-period mechanisms in determining year-class strength (May 1974).

Recent laboratory and field studies by Lasker et al. (1970) and Lasker (1975, 1978) indicate that survival of first-feeding larval northern anchovies, *Engraulis mordax,* may depend on several related factors: (1) the existence of fine-scale food strata containing high concentrations of properly sized food particles, (2) the coincidence of patches of larvae with adequate patches of food, and (3) the absence of predator populations sufficient to destroy the larval patches (Lasker and Smith 1977). On the principal anchovy spawning grounds off southern California, Lasker (1978) found that stability of the water column in the upper 30 m appeared to be a necessary condition for these fine-scale food strata. From additional survey data, Lasker (1981b) concluded that stability in the upper layers of the ocean during the anchovy spawning season is prerequisite to a successful year class. Wind-generated turbulent mixing associated with storms or strong coastal upwelling events destroys the required vertical stratification and patchiness, thereby contributing to increased larval mortality, which may result in a poor year class.

The purpose of this study is to describe the spatial patterns and annual cycles of climatological indices of wind-generated turbulent energy production and vertical stability in the California Current region. Bakun and Parrish (1980) suggested that information on the normal requirements for reproductive success of pelagic fishes might be obtained by comparing environmental conditions in the spawning areas with the conditions in regions where spawning does not usually occur. In this study, we compare monthly and seasonal indices of wind-generated turbulent mixing and upper ocean stability in the principal northern anchovy spawning areas to further explore the relationship of a stable ocean to larval survival, as described by Lasker (1981a). We will examine these indices in relation to the timing and locations of spawning of the three subpopulations of northern anchovy (Figure 1). To the extent that the mechanisms in Lasker's hypothesis exert a strong control on spawning success in the three subpopulations, there should be marked similarities among the wind-mixing and stability indices in all three spawning regions along the west coast of North America.

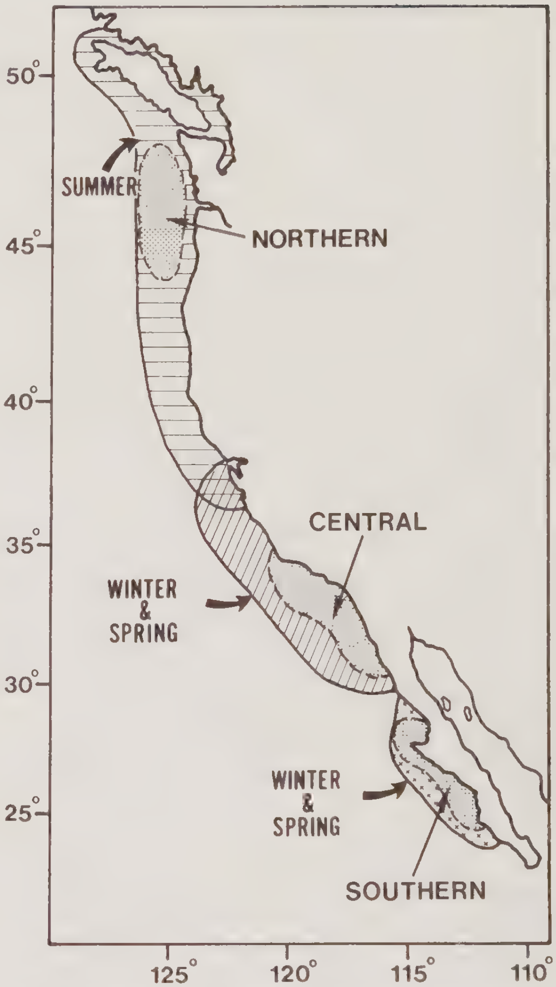

Figure 1. Geographic ranges (hatched), principal spawning areas (shaded), and seasons of the three subpopulations of northern anchovy, *Engraulis mordax*. Geographic ranges are modified from Smith and Lasker (1978) and Vrooman et al. (1981). Spawning areas have been inferred from egg and larvae distributions during the peak spawning months (Kramer and Ahlstrom 1968; Hewitt 1980; Richardson 1980).

DATA DESCRIPTION

Stability within the upper layers of the ocean is primarily determined by a balance between the net downward heat flux across the air-sea interface and turbulent mixing processes associated with wind-stirring and convective cooling. The evolution of transient and seasonal thermoclines can be predicted on the basis of the imbalance between the heat input from the atmosphere to the ocean and the intensity of turbulent wind mixing, which redistributes heat throughout the mixed layer. Strong surface heating during extended periods of light winds can produce strong stratification and rapid transitions to shallow mixed layers (Elsberry and Garwood 1978). Atmospheric forcing associated with winter storms or strong coastal upwelling "events" can destroy the stratification in the upper layers of the water column and rapidly deepen the "well-mixed" layer. Nelson (1977) and Nelson and Husby (in press) described the climatological distributions of surface wind stress and surface heat flux over the California Current region. This study extends the previous work to include summaries of an index of wind-generated turbulent energy production associated with redistribution of heat in the upper layers of the ocean and an index of upper-layer vertical stability resulting from surface heat flux and turbulent mixing processes.

Wind Mixing

The rate at which turbulent kinetic energy of the wind is added to the upper ocean and becomes available to mix the stable thermocline layers is proportional to the third power, or "cube," of the wind speed (Niiler and Kraus 1977). The proportionality factor is not well established and must be determined empirically from laboratory measurements and field calibrations. Because our main purpose is to make intraregional and seasonal comparisons, a sufficiently accurate index of the rate of turbulent energy production can be computed from the cube of the surface wind speed. Estimated and measured surface wind speeds were obtained from the historical surface marine weather observations archived in the National Climatic Center's (NCC) Tape Data Family-11 (TDF-11). This is the same set of data used by Nelson (1977) to compute surface wind stress and wind stress curl over the California Current.

Long-term monthly and quarterly means of the cube of the scalar wind speed were computed from all available surface marine reports from 1850 to 1972 for each 1-degree square area within a geographical region extending from 20°N to 50°N and from the west coast of North America to 10 degrees of longitude offshore. The same summary grid and editing procedures described by Nelson (1977) were adopted. Winter and summer quarters were chosen to approximately coincide with the peak spawning seasons for the southern, central, and northern subpopulations of the northern anchovy, respectively. Because we are interested in characterizing wind-generated turbulence in the important nearshore spawning habitats (Brewer and Smith 1982), long-term means were also computed for several partial 1-degree coastal squares that were not included in Nelson's (1977) wind stress distributions.

The principal sources of error in climatological means based on surface wind data are associated with imprecise Beaufort wind force estimates and nonuniform distributions of data in time and space (see Nelson 1977 for a discussion of errors). These errors are accentuated by computing the cube of a scalar variable. Sampling bias is even more critical to the stability index calculations (described in the next section) for which the available data are at least one order of magnitude less than the surface weather reports. Although each of the long-term monthly 1-degree square means is independent of all other months and squares, statistical independence is less important than the ability to present characteristic spatial and temporal distributions of wind speed cubed and vertical stability in the California Current. Therefore, when contoured fields have been used to display the results, the mean distributions were machine contoured, subjectively smoothed, and recontoured to remove "bull's-eyes" associated with extreme variability and inadequate sampling. Because most of the sampling error occurs offshore, this procedure should not substantially affect the conclusions for the nearshore regions.

Vertical Stability

Vertical stability of an oceanic water column depends on the vertical distribution of density, which is a function of temperature, salinity, and pressure. A water column is stably stratified if the density increases with depth. A commonly used index of the static stability of the water column, suggested by Hesselberg and Sverdrup (1915; cited in Sverdrup et al. 1942), is proportional to the vertical gradient of sigma-t, σ_t, (the density at atmospheric pressure):

$$E' = 10^{-3}\, d\sigma_t/dz \qquad (1)$$

The total expression for stability contains additional small terms related to the vertical gradients of temperature and salinity and the adiabatic temperature change due to compressibility. However, Hesselberg and Sverdrup (1915) have shown that stability in the upper 100 m is accurately expressed by Equation (1).

The computation of sigma-t requires values of temperature and salinity as a function of depth. The numbers of hydrographic stations that include vertical profiles of both temperature and salinity, over the entire California Current region, are rather small in terms of spatial and temporal coverage. For this reason, the more extensive set of mechanical bathythermograph (MBT) observations, which provide profiles of temperature versus depth, was used to compute an index of the vertical stability of the upper water column. The use of the vertical temperature structure to approximate the stability of the upper layer is valid if density depends primarily on temperature (i.e., little error will result in using only vertical temperature gradients to compute stability if the salinity is constant with depth or if the salinity gradients are small).

The waters flowing southward in the California Current are characterized by a shallow salinity minimum, which is due to the cool, low-salinity subarctic water mass being overrun from the west by the warmer, high-salinity subtropical water of the central Pacific anticyclonic gyre (Reid 1973). Figure 2 displays the January and June mean temperature-salinity (T-S) curves at standard depths to 500 m for three lines of 1-degree squares at 46°N, 33°N, and 27°N, respectively. The rightmost curves in each panel represent the 1-degree squares adjacent to the coast. These curves were derived from the National Oceanographic Data Center's (NODC) Station Data II file (SDII), including data to 1973.

The eastern North Pacific Ocean north of 40°N is influenced strongly by an annual excess of precipitation over evaporation, and the vertical salinity structure is characterized by a permanent halocline between 100 and 200 m (Tully 1964). Figure 2A shows this subarctic structure, particularly for the T-S curves 3 to 4 degrees of longitude offshore, where the upper 50-100 m is characterized by relatively uniform and low salinity values (32.5‰), below which there is an increase in salinity to a value of 33.8‰ at 200 m. The nearshore coastal waters off the Pacific Northwest are strongly influenced by the seasonal discharge of the Columbia River drainage basin. Peak discharges during May and June produce a large plume of low-salinity water (<32.0‰) in the upper 30 m; the plume extends toward the southwest from the mouth of the Columbia River (46°N) and can be distinguished as far as 500 km from shore (Barnes et al. 1972). Although the Columbia River plume is identified by low salinities in the surface layer, the distribution of the plume has been observed to be closely approximated by the 20-m isopleth of the thermal mixed layer depth during July (Owen 1968). During winter the region of diluted surface waters extends seaward about 50 to 100 km and from about 100 km south of the mouth of the Columbia River to the Strait of Juan de Fuca.

The cool subarctic waters in the California Current are modified by lateral mixing with the subtropical water mass to the west and by upwelling along the coastal margin (Tibby 1941). The first two 1-degree squares adjacent to the coast at 33°N (Figure 2B) are representative of conditions within the Southern California Bight. The seasonal changes in the upper 75 m of the water column are primarily due to the increase in solar insolation that contributes to the for-

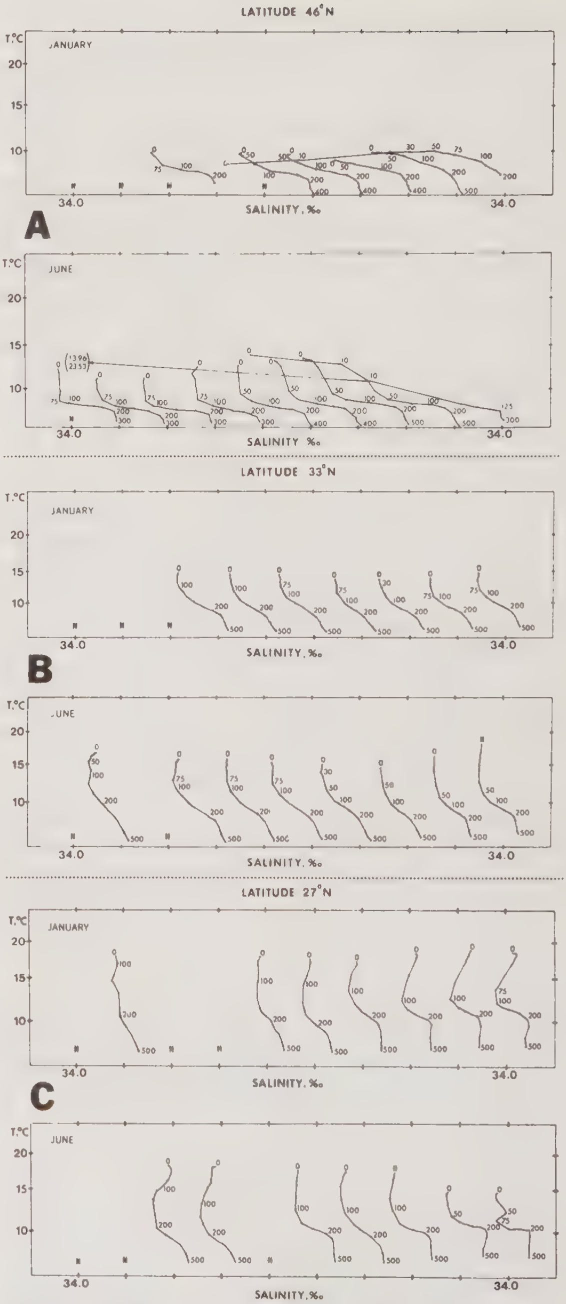

Figure 2. Mean temperature-salinity (T-S) curves for January and June for adjacent 1-degree squares from 10 degrees of longitude offshore to the coast at *(A)* 46°N; *(B)* 33°N; and *(C)* 27°N. In each diagram, the leftmost T-S curve corresponds to the 1-degree square located farthest offshore. The rightmost T-S curve corresponds to the 1-degree square closest to the coast. Each T-S curve is plotted relative to a salinity of 34‰ at each tick mark, and tick marks are spaced at intervals of 1‰. The depth in meters of particular T-S pairs is identified on each curve. The letter N denotes that no data were available to compute a mean T-S curve at that location.

mation of a strong near-surface thermocline. The salinity profile is relatively constant, with a slight decrease with depth down to 50-75 m. The effects of coastal upwelling are evident in the T-S curves 3 to 4 degrees of longitude offshore, where there is relatively little seasonal change in the T-S structure between January and June. The cool water upwelled farther north at Point Conception during early summer is advected toward the south; seasonal warming is suppressed. The T-S curves farther offshore reveal the effects of lateral mixing (between the subarctic water mass flowing south and the subtropical water mass to the west) in the increased salinities (33.0-33.5$^0/_{00}$) in the upper layers.

Farther south near Punta Eugenia (Figure 2C) the influence of an equatorial water mass is noted in the warmer, more saline ($\sim$34.5$^0/_{00}$) water in the 200-500-m depth range in the first four 1-degree squares adjacent to the coast. This water mass indicates the poleward flow of Equatorial Pacific water beneath the equatorward surface flow of the California Current (Reid et al. 1958). This warm, saline countercurrent has been traced as far north as the coast of Washington (Cannon et al. 1975; Reed and Halpern 1976). The effects of coastal upwelling are again evident in the much colder surface waters during June at the two squares adjacent to the coast. Excluding these coastal squares during the months of maximum upwelling (upwelling-favorable winds occur during the entire year off Baja California, and maximum upwelling occurs in April and May; Bakun and Nelson 1977), the T-S structure in the upper 100 m is characterized by relatively constant salinity or a decrease in salinity with depth to a minimum value at 75-100 m, and is associated with a strongly stratified temperature profile. The well-defined January subsurface salinity minima in the three squares adjacent to the coast may result from anomalous northward surface flow, which transports southern, high-salinity water into the region.

These seasonal mean T-S curves (Figures 2A, B, and C) do not completely describe the total range of temperature-salinity structures along the entire coast and particularly not in the offshore squares, where some T-S curves are based on data from only three hydrographic stations. However, these data adequately represent the modification of the subarctic water mass in the trajectory of the California Current from north to south, and the mixing of the shallow salinity minimum—which is found at a depth of 50 m near its source region at 47°N (Reid 1973)—with higher salinity water to the west and below the minimum.

The T-S curves reveal that in the vicinity of the central and southern subpopulations of the northern anchovy (Figure 2B, C), vertical stability in the upper 100 m can be closely approximated by the vertical distribution of temperature (i.e., salinity is nearly constant with depth). However, north of about 40°N, vertical stability in the near-surface layers is strongly influenced by a large increase in salinity with depth. The influence of excess precipitation over evaporation and freshwater discharge from the Columbia River is evident in winter. More marked effects are apparent during summer (Figure 2A), when the plume structure contributes to strong thermal stratification in the upper 20-30 m of the water column within 300-500 km of the coast. In this case, upper-layer temperatures increase while salinity decreases; both effects contribute to less dense water at the surface and stronger vertical density gradients in the upper water column. Although an index of stability computed just from temperature data underestimates the correct magnitude, our analyses of the mean T-S relationships suggest that temperature data alone can also be used to compute qualitative indices of vertical stability in the principal spawning area for the northern subpopulation of the northern anchovy.

The index of vertical stability was computed from the file of MBT profiles archived in the Master Oceanographic Observation Data Set (MOODS) at the U.S. Navy's Fleet Numerical Oceanography Center (FNOC), Monterey, California. Our extract of this file contains a rather complete set of approximately 131,000 MBT casts taken in the California Current between 1931 and 1975. However, a substantial number of the profiles are serial or near-replicate casts taken at the locations of weather ships, coastal lightships, and U.S. Navy radar picket ships, which operated in the eastern North Pacific Ocean from 1960 to 1965. To eliminate some of this station-specific sampling bias, we subsampled the data set by removing profiles obtained within 56 km (30 n mi) and 24 h of each other. This editing reduced the extract file to approximately 74,000 profiles. Over 90 percent of these profiles extended to at least 137 m (450 ft). The reduced data set contains between two and three times the numbers of profiles as the NODC SDII file. In addition, the MBT data provide better vertical resolution for the stability calculations than can be achieved from the standard-depth hydrocast data.

Two parameters were computed for each MBT profile extending deeper than 50 m: (1) the mixed layer depth (MLD) and (2) the strength of the first significant stratification, which we have termed "thermocline strength." The majority of the MBT profiles were digitized at intervals of 5 m. Mixed layer depth was defined as the upper limit of the first 5-m interval in which the temperature gradient ($\Delta T/\Delta Z$, Z positive downward) exceeded $-0.3°C$ per 5 m ($-0.06°C\ m^{-1}$). The layer of first significant stratification was identified as the first depth interval below the mixed layer where the vertical temperature gradient exceeded $-0.06°C\ m^{-1}$. The bottom of the thermocline was chosen to coincide with the upper depth of two successive 5-m intervals within which temperature gradients did not exceed $-0.06°C\ m^{-1}$. The index of thermocline strength was then calculated as the temperature difference between the MLD temperature and the temperature at the bottom of the thermocline. The relationships among MLD, bottom of the thermocline, and thermocline strength are shown schematically in Figure 3, which also depicts summer and winter thermal structure typical of the eastern North Pacific Ocean (Tully 1964).

Thermocline strength and mixed layer depth were summarized by 1-degree square areas and long-term months and quarters within the same 1-degree latitude-longitude grid used to compile the mean distributions of wind speed cubed. Because the numbers of subsurface data are an order of magnitude less than the observations of surface wind, the mean distributions of the two stability indices are substantially "noisier" than the distributions of wind speed cubed, particularly in the offshore areas. Some of the sampling "noise" in the contoured fields has been removed by subjective smoothing. Within the region most intensively studied by the CalCOFI surveys during the last 30 years, the subsurface data are adequate to define coherent spatial patterns of the stability indices.

DISTRIBUTIONS OF WIND-MIXING AND STABILITY INDICES

The three indices that have been summarized are bulk estimates of the intensity of wind-generated turbulence production and the strength of upper-layer stratification. The thermal MLD approximates the depth to which turbulent processes (expressed as wind speed cubed) dominate. Thermocline strength measures the magnitude of the density gradient (vertical stability) beneath the mixed layer, that is, in the seasonal (summer) and permanent (winter) thermocline (Figure 3). A possible linkage between these environmental conditions and successful year classes of the northern anchovy has been related to the existence of chlorophyll maximum layers (Lasker 1975, 1978), which are found in the thermocline and in the upper nutricline. Chlorophyll maxima lie somewhat deeper off Washington and Oregon (Anderson 1972) than off southern California (Reid et al. 1978; Cullen 1981). Low mean turbulence production and relatively high stability over a spawning season might favor persistent chlorophyll maxima; high turbulence production and low stability would not.

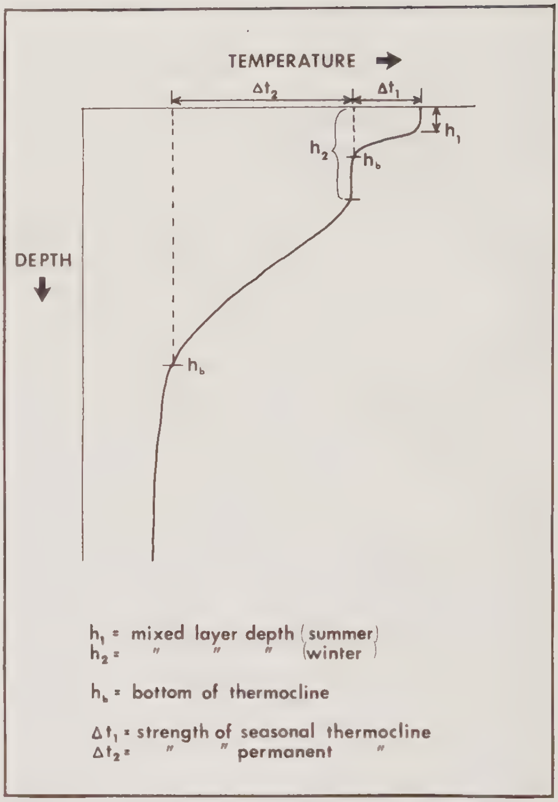
TEMPERATURE
Δt₂
Δt₁
h₁
h₂
h_b
h_b
DEPTH
h₁ = mixed layer depth (summer)
h₂ = " " " (winter)
h_b = bottom of thermocline
Δt₁ = strength of seasonal thermocline
Δt₂ = " " permanent "

Figure 3. Schematic profile of temperature versus depth depicting typical summer and winter mixed layer and thermocline structure.

Spatial Patterns

Distributions of wind speed cubed, thermocline strength, and mixed layer depth for winter (December-February, Figure 4A) and summer (June-August, Figure 4B) illustrate characteristic features of the locations and peak spawning periods for the central and southern subpopulations (winter-spring spawners) of northern anchovy and for the northern subpopulation (summer spawners). During winter (Figure 4A) low turbulence production, moderate to strong upper-layer thermal stratification, and relatively shallow mixed layer depths characterize (1) the nearshore region (from the coast to 100 km offshore) in the Southern California Bight and (2) a broad area extending toward the southwest from southern Baja California. Both regions correspond to the general spawning areas for the central and southern stocks (Figure 1), although the spawning grounds for the southern stock have not been

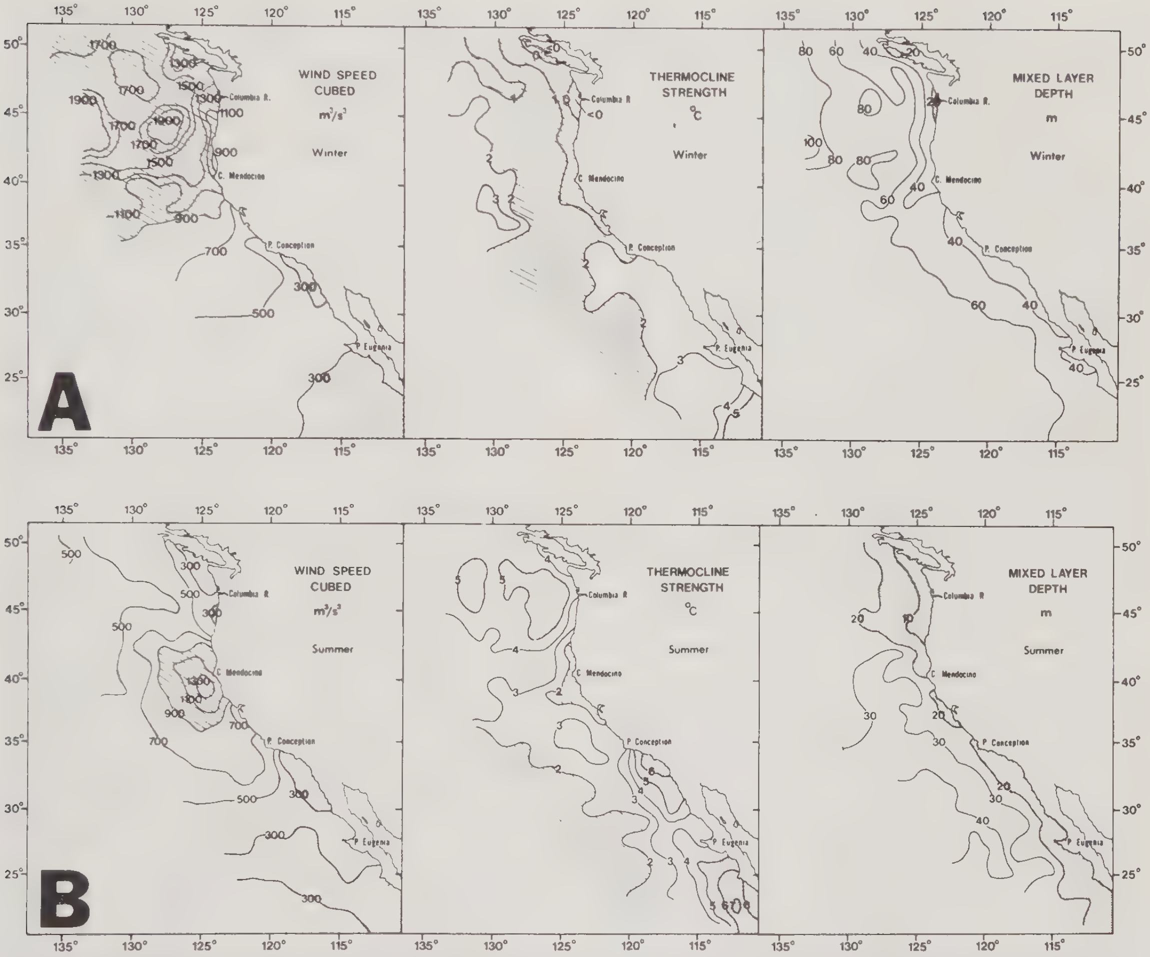
WIND SPEED CUBED
m³/s³
Winter
THERMOCLINE STRENGTH
°C
Winter
MIXED LAYER DEPTH
m
Winter
A
WIND SPEED CUBED
m³/s³
Summer
THERMOCLINE STRENGTH
°C
Summer
MIXED LAYER DEPTH
m
Summer
B
Columbia R.
C. Mendocino
P. Conception
P. Eugenia
135°
130°
125°
120°
115°
50°
45°
40°
35°
30°
25°

Figure 4. Mean distributions of wind speed cubed (m^3s^{-3}) indicating the rate of turbulent energy production, thermocline strength (°C), and mixed layer depth (m) for *(A)* winter (December-February) and *(B)* summer (June-August). Wind speed cubed is contoured at intervals of 200 m^3s^{-3}. Values less than 300 m^3s^{-3} are shaded, and values greater than 900 m^3s^{-3} are hatched. Thermocline strength is contoured at intervals of 1°C. Shaded areas are greater than 5°C; hatched areas denote a thermocline strength less than 2°C. Mixed layer depth is contoured every 20 m, and values less than 20 m are shaded.

completely described. Lower values of wind speed cubed (<200 m^3s^{-3}), stronger stratification, and shallower mixed layers (~30 m) occur close to the coast. The local spatial minimum in wind-generated turbulence in the Southern California Bight persists throughout the year and is consistent with a decrease in the magnitude of the equatorward surface wind in the lee of Point Conception. A nearshore maximum in wind speed cubed just south of Punta Baja (near 30°N values approach 500 m^3s^{-3}) corresponds to a permanent region of negative wind stress curl that reaches the coast in the vicinity of Punta Eugenia (Nelson 1977). High turbulence production, weak stratification, and deep mixed layers characterize the entire region north of San Francisco, with the exception of a small area off the mouth of the Columbia River, for which mixed layer structure is not completely defined by temperature alone (see Figure 2A).

The similarities among the distributions of wind speed cubed and the two indices of upper-layer stratification are obvious in summer (Figure 4B). South of Point Conception, the two regions of low turbulence production are associated with shallow mixed layers (~20 m) and the highest values of thermocline strength. These features (i.e., high stability in combination with low turbulence) are not particularly well related to the central stock's spawning cycle, which passes through a minimum between July and

October (Smith and Richardson 1977). This simply indicates that factors other than the simultaneous occurrence of low turbulence and high stability influence the timing of peak spawning. The highest values of wind speed cubed occur in the region of maximum upwelling off Cape Mendocino, which is also characterized by the weakest stratification. Off the Columbia River there is a strong correspondence between the patterns of wind speed cubed, thermocline strength, and mixed layer depth and Richardson's (1980) distributions of eggs and larvae of the northern subpopulation of *E. mordax*. The strong influence of the Columbia River plume is apparent in the high values of thermocline strength and the shallowest thermal MLD's in the entire California Current region. It is possible that, because of this strong upper-layer stratification, higher values of turbulence production may be associated with spawning success for the northern subpopulation in summer (e.g., the area within the 500 m^3s^{-3} contour off Vancouver Island, Washington, and Oregon, Figure 4B) than for the central and southern subpopulations in winter (Figure 4A).

Seasonal Variability

Annual cycles of wind speed cubed (Figure 5A, B) and thermocline strength (Figure 5C) are shown for selected 1-degree squares near the principal spawning grounds for the three subpopulations of the northern anchovy. A strong correspondence between the timing of peak spawning and the magnitude of the mean wind-generated turbulence can be demonstrated for each of the three regions. However, the relationship of the spawning cycle to the annual cycle of vertical stability (thermocline strength) shows less consistency between regions.

The southern stock spawns off southern Baja California (25-28°N) during winter and spring; peak larval abundance occurs from January to March (Smith 1972). Wind speed cubed fluctuates about a nominal value of 300 m^3s^{-3} from September to February (curve 1, Figure 5A); mean values exceed 400 m^3s^{-3} after the onset of upwelling-favorable winds in March and April (Bakun and Nelson 1977). During this period, thermocline strength decreases from a maximum (>6°C) in October to a minimum (~0-1°C) in January (curve 1, Figure 5C).

The central stock spawns in the Southern California Bight (30-34°N) throughout the year, with a maximum from February to April (Smith and Richardson 1977). The Southern California Bight is characterized by uniformly low turbulence production throughout the year (curve 2, Figure 5A). At this location, the small peak in the annual cycle (~300 m^3s^{-3}) occurs during the peak spawning season; thermocline strength is nearly constant, but at a minimum (~2°C), from January to April (curve 2, Figure 5C). The seasonal

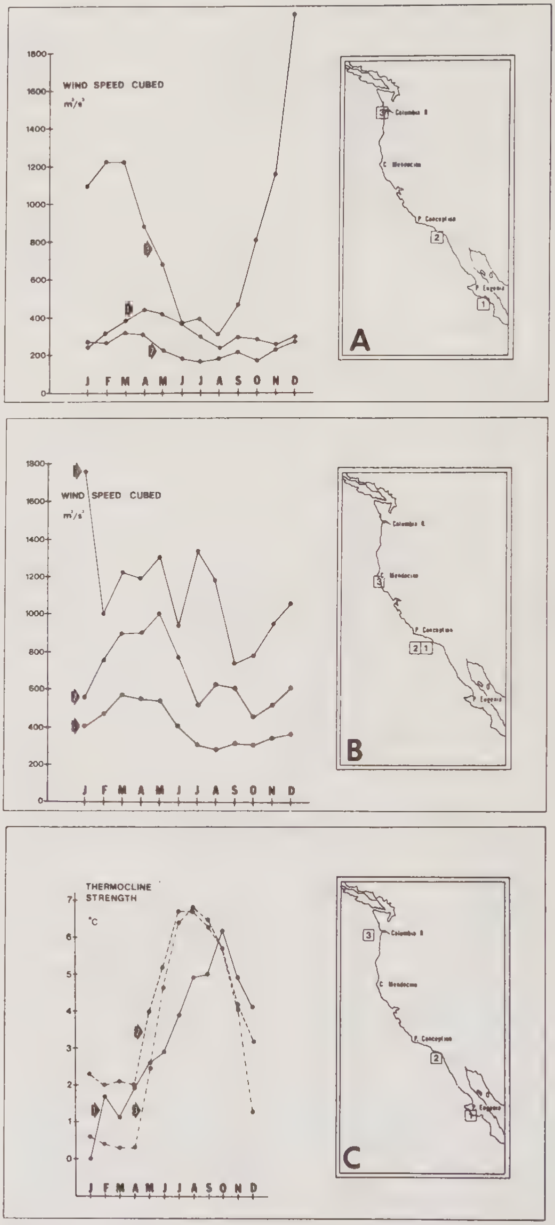

Figure 5. Annual cycles of wind speed cubed (m^3s^{-3}) and thermocline strength (°C) at selected 1-degree squares along the coast. Characteristic values of wind speed cubed and thermocline strength in the three northern anchovy spawning areas are shown in panels *A* and *C*. Mean values of wind speed cubed typical of the offshore regions of the Southern California Bight and the region of maximum upwelling off Cape Mendocino are displayed in panel *B*.

transition to a shallow mixed layer structure (i.e., strong upper-layer stratification) occurs between April and May, but the precise timing of the transition period cannot be resolved by these long-term mean data. According to Richardson (1980), the northern stock spawns in the Columbia River plume (44-46°N) from June to August; spawning is concentrated in July. Off the mouth of the Columbia River, upper-layer stratification increases to a maximum (6-7°C) from July to September (curve 3, Figure 5C). It is also notable that mean wind speed cubed decreases to a minimum (350-400 m^3s^{-3}) through the spawning season (curve 3, Figure 5A).

Taken in isolation, these data suggest a relationship between peak spawning periods and optimum levels (not necessarily minimum levels) of wind-generated turbulent mixing. We note that the cube roots of the mean values associated with the spawning seasons (200-400 m^3s^{-3}) lie close to an apparent low wind-speed threshold for the formation of oceanic whitecaps (Monahan 1971), a more obvious, visual index of wind-generated turbulence production. In this context, the proper relationship between the mean wind speed cubed and the mode of the wind-speed probability distribution (which typically shows Poisson rather than Gaussian behavior) is important. From an examination of selected frequency distributions presented by Nelson (1977), we concluded that mean values of 200-400 m^3s^{-3} are entirely consistent with modal wind speeds in the range 3-5 m s^{-1}. This range of values is just below the threshold wind speed ($\sim$5 m s^{-1}) that Therriault and Platt (1981) used to distinguish biological (low turbulence) from physical (high turbulence) control of phytoplankton patchiness.

The data plotted in Figure 5B demonstrate a large offshore increase in turbulence production in the Southern California Bight (curves 1 and 2) and illustrate the seasonal progression of wind speed cubed that characterizes the region of maximum upwelling (curve 3). The zonal section represented by curve 2 (Figure 5A) and curves 1 and 2 (Figure 5B) shows a monotonic increase in wind speed cubed from values less than 300 m^3s^{-3} near the coast to values exceeding 900 m^3s^{-3} offshore. The amplitude of the annual cycle is substantially larger at the offshore locations as well. Off Cape Mendocino, wind-generated turbulence production is high throughout the year; highest values are associated with winter storms and strong equatorward surface winds during summer.

Seasonal isogram plots of wind speed cubed and thermocline strength (Figure 6A) and two independent estimates of mixed layer depth (Figure 6B) were constructed from the long-term monthly mean values within 3 degrees of the coast. Wind speed cubed was plotted for the 1-degree squares immediately adjacent to the coast. The stability indices were averaged over three 2-degree squares at each latitude to increase the number of observations per averaged value.

The seasonal cycles of wind speed cubed and thermocline strength (Figure 6A) show strong similarities among the timing and locations of regions characterized by low wind-induced turbulence ($<$300 m^3s^{-3}) and strong vertical stability (thermocline strength $>$5°C). The relative minima (wind speed cubed) and maxima (thermocline strength) in the time-space domain nearly coincide with the known spawning periods and spawning grounds for the northern anchovy. The notable exception occurs between 30°N and 35°N in the Southern California Bight.

The coastal region between 43°N and 48°N is characterized by low turbulence and strong upper-layer stratification from June to September. During this same period, the thermal MLD's are less than 20 m over the entire region north of 40°N (Figure 6B). Minimum MLD's occur in May and June in response to peak freshwater discharge from the Columbia River. Between Cape Mendocino (40°N) and Point Conception (35°N) high values of wind speed cubed, low stability, and shallow mixed layers are associated with strong coastal upwelling during spring and summer. During winter, frequent and severe storms cross this region (north of 40°N), drive the mixed layer deeper (Figure 6B), and decrease upper-layer stratification to a minimum (Figure 6A).

Because of the strong influence of the Columbia River plume on vertical stability, we checked the consistency of the thermal mixed layer depths (based on MBT data) by constructing a seasonal isogram plot of pycnocline depth. Pycnocline depth was defined as the upper depth of the interval for which stability (defined by Equation 1) was a maximum, and mean values were computed from the hydrographic data in the NODC SDII file. Comparison of the two panels in Figure 6B shows close agreement between thermal MLD and pycnocline depth along the entire coast during the summer. A weaker relationship is evident during winter, although the two methods show similar seasonal trends.

The nearshore region in the Southern California Bight (30-35°N) is characterized by uniformly low values of wind speed cubed ($<$300 m^3s^{-3}) throughout the year, with the exception of a local maximum at 33°N from February to April (Figure 6A). Upper-layer stratification follows a well-defined, large-amplitude annual cycle. There is a lack of agreement between the peak spawning period for the central subpopulation of *E. mordax* (January-April) and maximum thermocline strength (July-September). Thus the simultaneous oc-

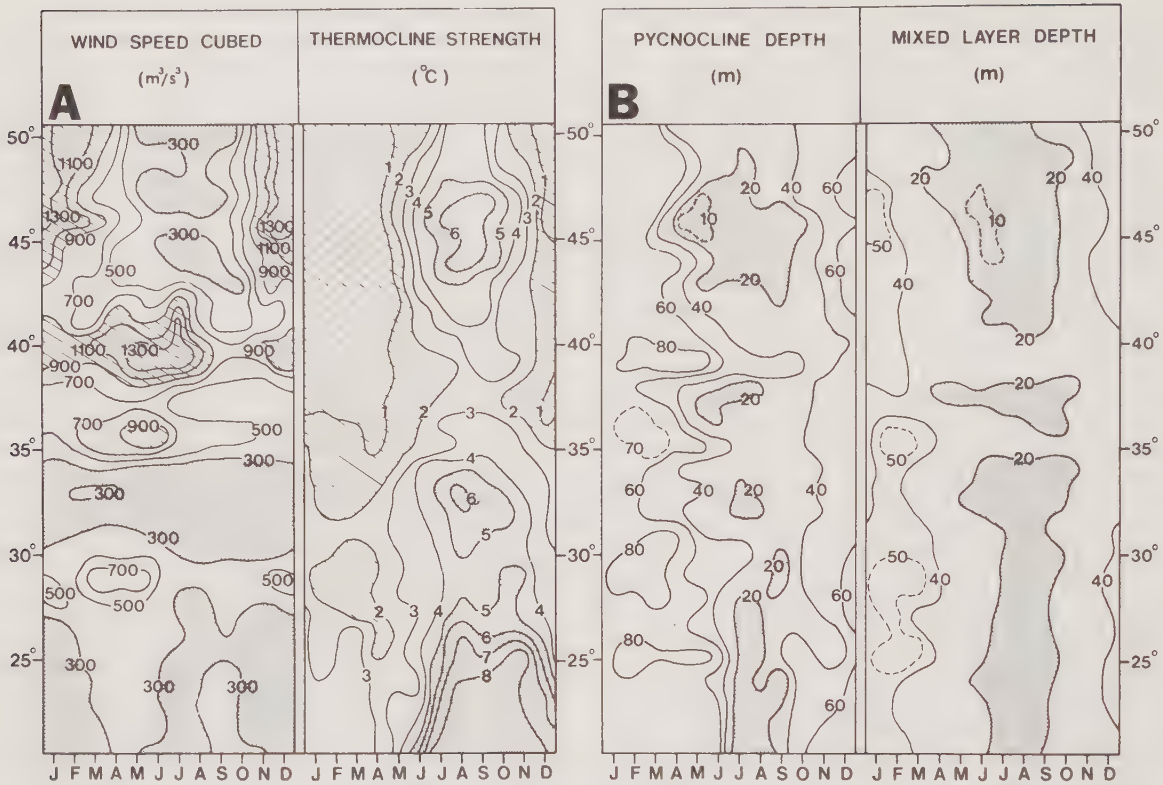

Figure 6. Seasonal cycles of (*A*) wind speed cubed (m^3s^{-3}) and thermocline strength (°C) and (*B*) pycnocline depth (m) and mixed layer depth (m) near the coast. Means of wind speed cubed were computed by month for 1-degree squares immediately adjacent to the coast. Monthly means for thermocline strength, pycnocline depth, and mixed layer depth are averages of the values within 3 degrees of the coast at each latitude. In panel *A*, wind speed cubed is contoured at intervals of 200 m^3s^{-3}. Values less than 300 m^3s^{-3} are shaded, and hatched areas correspond to mean values greater than 900 m^3s^{-3}. Thermocline strength is contoured every 1°C. Shaded areas are greater than 5°C; hatched areas are less than 2°C. In panel *B*, pycnocline depth and mixed layer depth are contoured every 20 m. Layer depths less than 20 m are shaded.

currence of high stability and low turbulence may not be necessary for spawning success. This also suggests that high stability (and shallow mixed layers) prior to or during the peak spawning months may also contribute to adverse spawning conditions, for example, by inhibiting the upward flux of nutrients into the mixed layer and thereby decreasing primary production.

South of 30°N, a pattern of low turbulence production is broken twice over the annual cycle: (1) from March to June in conjunction with strong, upwelling-favorable surface winds, and (2) during the fall when tropical storms occasionally impinge on Baja California. This region is also characterized by relatively strong thermal stratification (values exceed 3°C; maximum stability occurs from August to November, Figure 6A) and shallow mixed layers (20-40 m) throughout the year. If upper-layer stability and wind-generated turbulent mixing were the only two factors associated with the "critical period" for larval anchovies, then the extended period of low turbulence and relatively high stability near the coast and south of 27°N suggests that spawning conditions might be more favorable for the southern subpopulation than for the central stock. Of course, other factors, such as the spatial structures of predator-prey populations (Smith and Lasker 1978), may interact with the processes addressed in this paper to regulate spawning success, particularly in regions of low mean values of wind speed cubed (e.g., in the Southern California Bight).

Turbulence, Transport, and Stability on the Principal Spawning Grounds

The long-term mean distributions mapped in Figures 4-6 corroborate Lasker's (1975, 1978) explanation of the "critical period" concept (i.e., a stable ocean in the absence of turbulent mixing is a prerequisite for larval survival). The spawning grounds for each of the three subpopulations of the northern anchovy are characterized by low values of wind speed cubed during the peak spawning seasons; mod-

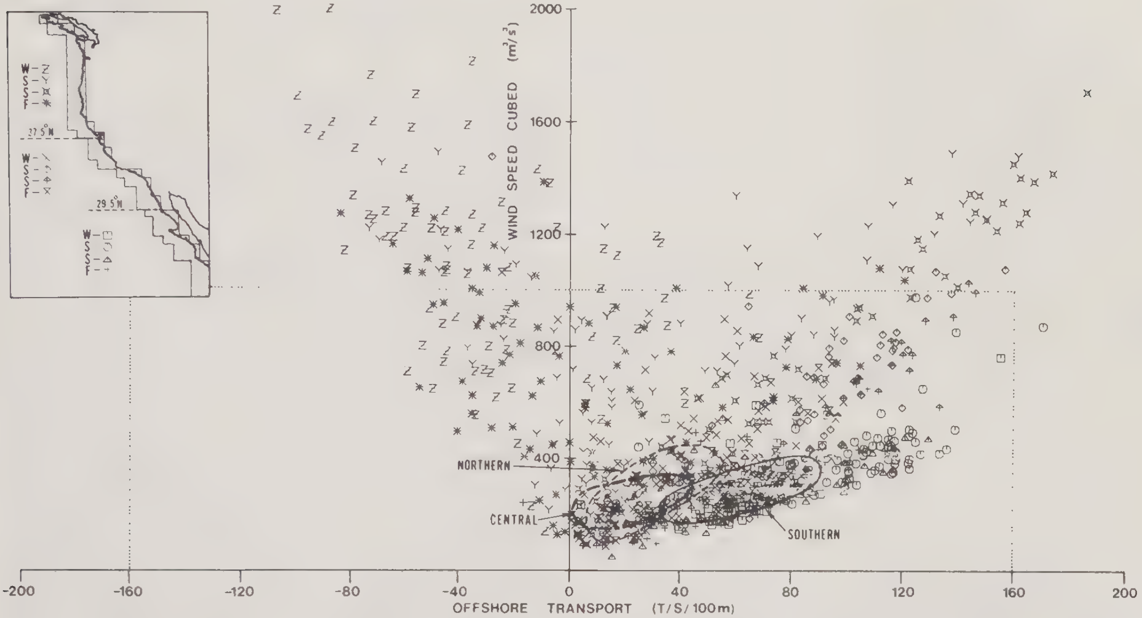

Figure 7. Scatter diagram of wind speed cubed (m^3s^{-3}) versus offshore Ekman transport ($t\ s^{-1}$ per 100 m). Mean monthly values are plotted for each 1-degree square within the shaded region shown in the inset. Negative values denote onshore transport. Symbols are coded according to season (W,S,S,F) within each of the three coastal regions shown in the inset. Winter corresponds to December-February. Values of wind speed cubed and offshore transport associated with the peak spawning months and spawning grounds for the southern, central, and northern subpopulations of *E. mordax* are enclosed by solid, dashed, and dotted lines, respectively. The dotted lines at 1000 m^3s^{-3} and ± 160 $t\ s^{-1}$ per 100 m correspond to the limits of the expanded scatter diagrams in Figure 8.

erate to strong upper-layer stratification is associated with two of the three spawning seasons and locations. During the peak spawning season for each subpopulation, low values of wind speed cubed correspond to equatorward surface wind stress (Nelson 1977), implying some degree of offshore transport in the surface layers and upwelling near the coast. Surface transport has been discussed (Parrish et al. 1981) as an alternate but not mutually exclusive "critical period" hypothesis. Therefore, an index of offshore Ekman transport was used as an additional variable to characterize the wind field over the principal spawning grounds.

Scatter diagrams of turbulence versus transport were constructed by plotting the long-term monthly mean values of wind speed cubed against estimates of offshore Ekman transport (Figures 7 and 8). Nelson's (1977) surface wind-stress values were used to compute the offshore directed component of surface Ekman transport (using the method described by Bakun and Nelson, 1977) for each 1-degree square area within a region extending from the coast to 2 degrees of longitude offshore. The total ensemble of approximately 720 possible monthly mean pairs of wind speed cubed and offshore transport was partitioned into three geographic regions with breaks at 29.5°N and 37.5°N (approximate stock boundaries) and into four quarters, with winter defined as December-February. Twelve different symbols were used to distinguish the spawning seasons and spawning grounds. The total data set was subsampled and replotted in four additional scatter diagrams to illustrate the salient points more clearly (Figure 8). Different letter symbols are shown in Figure 8, analogous procedures were used to construct the diagrams. Each of the points plotted in these diagrams corresponds to a pair of long-term monthly means. Sampling variability produces large scatter about the means. Thus, these diagrams do not represent all possible combinations of turbulence and transport and should be considered as mean "envelopes" characterizing the average environmental conditions in the region.

Low turbulence and weak offshore transport are common to all three spawning regions (Figure 7), which occupy overlapping positions near the origin in the diagram. Four distinct regimes are evident in this diagram: (1) the entire left portion (i.e., onshore transport) is characteristic of fall-spring off the Pacific Northwest; (2) the high wind speed cubed/high offshore transport region (i.e., greater than 600 m^3s^{-3} and 80 $t\ s^{-1}$ per 100 m) distinguishes the region of maximum upwelling from Point Conception (35°N) to Cape Blanco (43°N) in spring and summer; (3) the

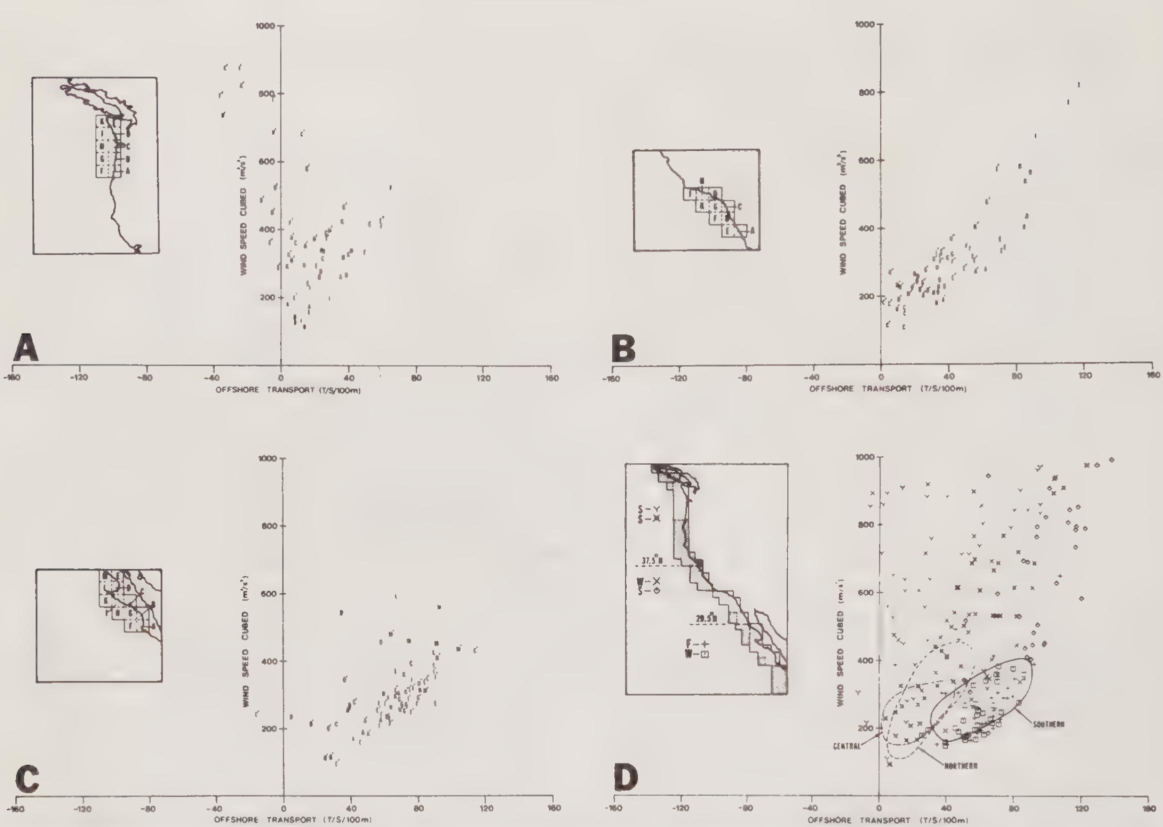

Figure 8. Scatter diagrams of wind speed cubed (m^3s^{-3}) versus offshore Ekman transport (t s^{-1} per 100 m) in the (*A*) northern, (*B*) central, and (*C*) southern spawning regions. Values for the nonspawning areas are plotted in panel *D*. Mean monthly values are plotted for March-August in panel *A*; December-May in panel *B*; and September-February in panel *C*. Negative values denote onshore transport. Symbols are coded according to the location of the 1-degree squares shown in the insets, and primed letters correspond to the first three months of the six months plotted in each of panels *A*, *B*, and *C*. Values plotted in panel *D* correspond to the shaded regions outside the principal spawning areas (inset), but during the peak spawning seasons in each of the three regions. The symbols are coded according to season (W,S,S,F) and region, and the enclosed portions of the scatter diagram labeled northern, central, and southern are the same as those shown in Figure 7. Note the change of scale for wind speed cubed in this figure compared to Figure 7.

low-turbulence/high transport area is associated with the Baja California upwelling system in the spring; and (4) the low wind speed cubed/weak offshore transport region (i.e., less than 400 m^3s^{-3} and 80 t s^{-1} per 100 m) almost exclusively encompasses data from the principal spawning regions during the peak spawning seasons. The overlap among the three spawning regions would have been more pronounced if we had plotted wind speed cubed against the alongshore component of surface stress (thereby removing the effect of latitudinal variation in the Coriolis parameter; offshore transport is inversely proportional to the Coriolis parameter f, where f = 0.0001458 SIN ϕ s^{-1} and ϕ is the geographic latitude).

Separate scatter diagrams were constructed for each of the three principal spawning regions but only for the 6 months spanning the spawning season in each region (Figure 8A, B, and C). Data for the nonspawning regions during the same 6-month periods are plotted in Figure 8D to identify other coastal locations characterized by low turbulence and weak offshore transport. Our interpretation of these scatter diagrams follows the main conclusion drawn from the spatial and temporal distributions: the months and locations associated with low wind-generated turbulence (and weak offshore transport) are also the principal spawning seasons and spawning grounds for each of the three subpopulations of the northern anchovy.The lowest values of wind speed cubed and offshore transport correspond to the squares immediately adjacent to the coast (e.g., symbols A, B, C, D, and H in Figure 8B). Examination of anchovy larvae distributions for 1966-1979 (Hewitt 1980) suggests a tendency for higher larval abundance within 100 km of the coast than offshore, which would be consistent with greater spawning success in the nearshore, low-turbulence regions.

There are a few locations and months for which the mean wind speed cubed/offshore transport pairs fall within the areas on the diagrams occupied by the spawning stocks (Figure 8D). For the southern stock, most of these data are from 1-degree squares located well offshore (e.g., the entire shaded block south of Cabo San Lucas at 25°N). Virtually no other locations between 29.5°N and 37.5°N can be characterized by the low-turbulence/weak transport values associated with the central stock's spawning grounds. The additional data coinciding with the position occupied by the northern stock come from the 1-degree squares adjacent to Vancouver Island and from the nearshore region in the vicinity of San Francisco. Recent data suggest that the coastal waters adjacent to San Francisco Bay provide a suitable habitat for winter-spring spawning of *E. mordax* (Stepanenko 1981[1]).

Analogous procedures were used to construct a scatter diagram of wind speed cubed versus thermocline strength (Figure 9). For this diagram, quarterly mean values of wind speed cubed and thermocline strength were used. Thus the numbers of wind speed cubed/thermocline strength data pairs have been reduced by a factor of three relative to the data points plotted in Figure 7. Although this particular diagram shows a great deal of scatter, there is evidence for an inverse relationship between wind speed cubed (turbulence) and thermocline strength (stability). High turbulence (large wind speed cubed) and weak stability (low thermocline strength) correspond to winter storm activity and deep mixed layers off the Pacific Northwest, although similar turbulence/stability conditions occur off Cape Mendocino during spring and summer. High stability and relatively low values of wind speed cubed characterize Baja California in the fall (symbol D, Figure 9). The majority of the months and locations associated with the peak spawning seasons on each of the spawning grounds (symbols A, B for the southern stock; E, F for the central stock; L for the northern stock) lie within a relatively narrow range of values for wind speed cubed (200-400 m^3s^{-3}) and thermocline strength (2-5°C). This is evident in the close agreement among the three envelopes enclosing these points for each stock. For similar values of wind speed cubed in each region, stability (thermocline strength) is slightly higher on the spawning grounds for the southern and northern stocks of *E. mordax* than for the central stock.

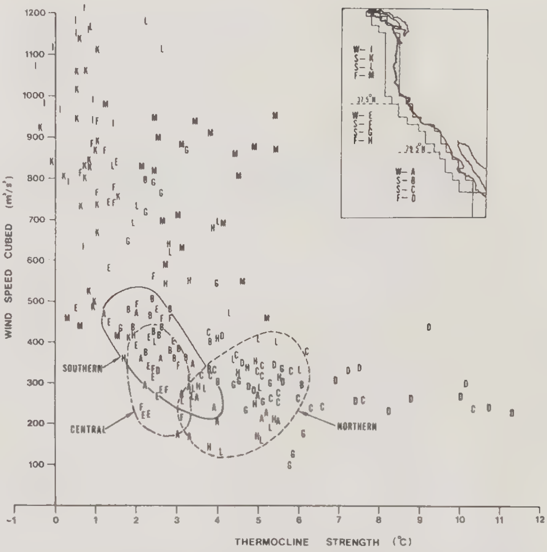

Figure 9. Scatter diagram of wind speed cubed (m^3s^{-3}) versus thermocline strength (°C). Mean quarterly values are plotted for each 1-degree square within the shaded region shown in the inset. Symbols are coded according to season (W,S,S,F) within each of the three coastal regions. Winter corresponds to December-February. Values of wind speed cubed and thermocline strength associated with the peak spawning months and spawning grounds for the southern, central, and northern subpopulations of *E. mordax* are enclosed by solid, dashed, and dotted lines, respectively.

DISCUSSION

Historical surface wind observations and subsurface temperature data from the California Current region have been used to compile long-term monthly mean distributions of two indices related to (1) the rate of turbulent energy production by the wind (wind speed cubed), and (2) the vertical stability of the upper water column (thermocline strength). Characteristic spatial patterns (Figure 4) and annual cycles (Figures 5 and 6) of these indices were discussed in relation to the principal spawning grounds and peak spawning seasons of the three subpopulations of the northern anchovy, *Engraulis mordax*. A strong correspondence was shown among the locations and seasons characterized by low wind speed cubed (turbulent mixing) and the timing of the spawning cycle for each stock. A weaker correspondence of the spawning cycle to relatively high thermocline strength (vertical stability) was demonstrated. Each of the spawning regions in the California Current is also associated with weak coastal upwelling and offshore transport during the respective spawning season (Figures 7 and 8). Bakun and Parrish (1982) show similar relationships among the regions of low turbulence production and the principal spawning grounds of the Peruvian anchoveta, *Engraulis ringens*.

One interpretation of these long-term mean data is that reproductive strategies have evolved in response to "optimum" levels of turbulent mixing in the stable layers of the upper ocean, rather than to minimum levels of turbulence (or to maximum vertical stability). There are two important aspects to this rationale. In the complete absence of wind stirring or (upwelling), nutrient fluxes into the mixed layer would be substantially reduced, and phytoplankton production would decrease. Therefore, some degree of mixing and entrainment of nutrients at the base of the mixed layer would be required to maintain adequate concentrations of food for first-feeding larval anchovies. On the other hand, if the "optimum" level of turbulent mixing was frequently exceeded by large amounts, then destruction of fine-scale food strata and dispersion of larval anchovies could lead to recruitment failure, particularly if unfavorable conditions persisted through the spawning season (Lasker 1978). A similar argument can be made that too much stability prior to or during a spawning season might produce equally adverse spawning conditions by severely inhibiting the upward flux of nutrients and reducing primary production. There is evidence to suggest that the long-term monthly mean values of wind speed cubed that characterize the spawning grounds of the three subpopulations of *E. mordax* are consistent with a "threshold" wind speed (~ 5 m s^{-1}) associated by Kullenberg (1978) and Therriault and Platt (1981) with horizontal patchiness in phytoplankton distributions.

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[1] Stepanenko, M.A. Assessment of stocks and reproduction conditions of some commercial fish off the Pacific coast of the North America in 1980. Mimeograph report, Pacific Research Institute of Fisheries Oceanography (TINRO), Vladivostok, 1981, 21 p.

Mean distributions of environmental indices, which represent highly nonlinear, time-dependent physical processes (e.g., wind speed cubed), are meaningful to investigations of recruitment variability if, for example, pattern recognition can be used to identify normal requirements for reproductive success. In this context, the spatial patterns and annual cycles of wind speed cubed and thermocline strength discussed in this paper are useful, and corroborate Lasker's experimental evidence (1975, 1978). However, to determine the degree to which turbulence and stability have exerted a limiting control on spawning success of the northern anchovy over the past 14 years, reasonably complete time series data, on space and time scales appropriate to the biological processes, are required. Because the linkage between the physical processes (wind speed cubed) and recruitment success (year-class strength) is by no means direct, it is not reasonable to expect "any single mechanism to explain larval survival in all cases" (May 1974).

A 14-year time series (1968-81) of daily mean wind speed cubed indices (Figure 10) was constructed for a representative location in the Southern California Bight (33°N, 119°W). An estimate of the surface wind was computed from the 6-hourly northern hemisphere surface pressure analyses available at Fleet Numerical Oceanography Center, using the method described by Bakun (1973). The daily values displayed in Figure 10 are means of the cube of the wind speed for the four synoptic samples per day. These time series data are characteristic of physical processes integrated over spatial scales (typically 3-degree resolution) which are 1 to 2 orders of magnitude larger than the horizontal scales associated with plankton patchiness and larval feeding. The indices are also uncalibrated in terms of absolute magnitude (Bakun 1973). Nevertheless, we feel that the analyzed meteorological fields offer a means of reconstructing consistent time-histories of the physical processes (e.g., wind speed cubed, offshore transport) that may have limited recruitment, thus causing the wide variations in year-class size over the past 14 years of the anchovy fishery. A similar time series of the stability indices could not be assembled because appropriate subsurface data do not exist.

The striking features of the daily wind speed cubed series are the large pulses over relatively restricted time periods during the spawning season (December-April). The characteristics distinguishing the spawning season of one year from that of another seem related to the frequency of occurrence of wind speed cubed "events" above a threshold value. In terms of Lasker's first-feeding hypothesis, favorable spawning seasons leading to strong year classes (e.g., 1976, 1978) contain relatively fewer events of magnitude exceeding a critical value, whereas spawning seasons resulting in poor year classes (e.g., 1975, 1977) are characterized by relatively more frequent, extended periods of intense wind events. Indeed, the first-feeding hypothesis has been largely formulated on the basis of field observations obtained before and after a period of strong winds during 1975 (Lasker 1975, 1978) and during the drought year spanning the 1975-76 spawning season (Lasker 1981b). Interestingly enough, the period of strong winds in February 1975 (also a period of strong upwelling) was followed by an even more intense mixing event (also strong upwelling) near the end of March—the largest such event during the spawning season over the 14-year record. It is likely that the occurrence of both of these events within one month contributed to the highest estimated recruitment failure in the history of the anchovy fishery (Smith et al. 1981).

One simple way of reducing the daily time series data to a quantitative index relating to the history of the fishery is to integrate the wind speed cubed index over the spawning season (i.e., form the December-February mean). These values (or the means for several different combinations of months from December

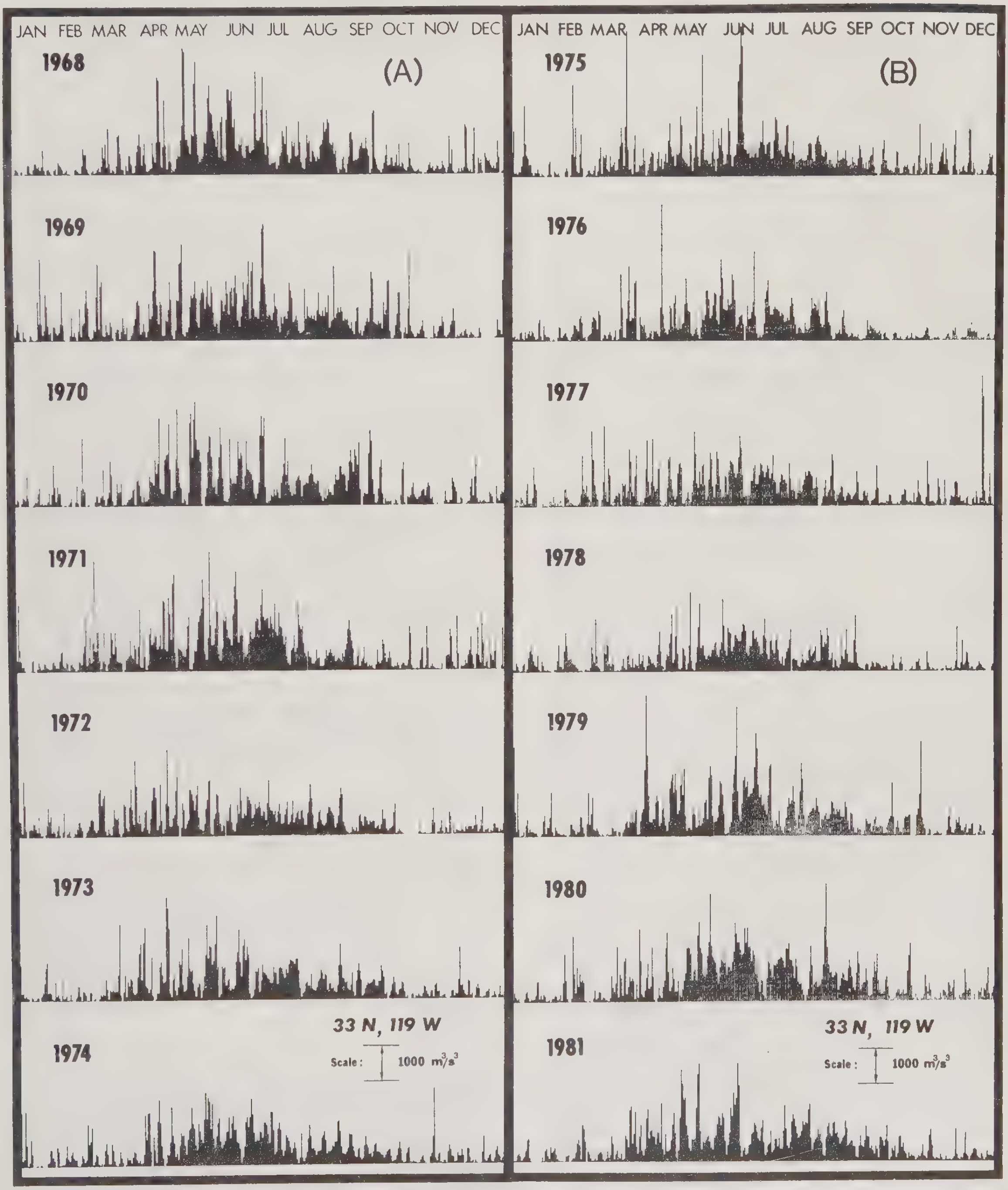

Figure 10. Daily indices of wind speed cubed (m^3s^{-3}) at 33°N, 119°W for *(A)* 1968-74, and *(B)* 1975-81. Daily values were derived from 6-hourly surface atmospheric pressure analyses. Values are scaled according to the key on each plot.

to April) could be used to test the relationship of wind-induced turbulence to recruitment and year-class strength, for example, by regressing the values of the intensity of wind speed cubed, averaged over the spawning season, against estimates of year-class size (Mais 1981) or by using rank correlation methods to compare the relative ranks of wind speed cubed with relative ranks of spawning success (Smith et al. 1981). Such statistical tests are beyond the scope of this paper. However, it is unlikely that the variability in year-class strength would be well described by a linear correlation with bulk estimates of a highly nonlinear process, particularly considering the limited degrees of freedom in the data.

This is not to imply that turbulence and stability may not exert a control on spawning success (i.e., the lack of a significant statistical relationship would not be sufficient to reject the wind-turbulence hypothesis), but rather to suggest that the mean intensity of wind speed cubed over the spawning season may not provide a useful way to quantify the integrated effects of physical processes on time scales critical to larval first feeding. A simple calculation demonstrates our point. A sequence of 30 days in which the (uncalibrated) daily wind speed cubed averages 300 m^3s^{-3} would have exactly the same monthly mean as a sequence of 30 days in which periods of 4 days with daily means of 125 m^3s^{-3} are followed by an event of magnitude 1000 m^3s^{-3}. In the first situation, mixing and stability conditions would most likely favor the formation of chlorophyll maximum layers, leading to recruitment success. In the second case, recruitment failure would result from episodic destruction of stratified layers during the critical period (2-3 days) after yolk-sac absorption (Lasker et al. 1970).

It is likely that the most favorable conditions for larval survival correspond to extended periods of low-turbulence "windows" prior to and continuing through the critical period. In terms of this requirement, at least five important features in the wind speed cubed time series need to be quantified in relation to the "critical period" requirements of larval anchovy: (1) the required length of the low-turbulence "windows," (2) the magnitude and duration of events exceeding the low-turbulence threshold, (3) the frequency with which high-turbulence events recur, (4) the association of high-turbulence events with coastal upwelling or downwelling processes, and, perhaps most important, (5) the timing of the spawning cycle in relation to the sequence of turbulence events. A proper analysis of the last feature would require detailed information on the birthdate distributions of surviving anchovy (Methot 1981).

We suggest two methods that might be used to further investigate the effects of physical mechanisms on reproductive success. A statistical approach could be used to search through a time series of daily (or 6-hourly) values of wind speed cubed, to find the combinations of low-turbulence "windows" and high-turbulence "events" that best characterize a spawning season as favorable or unfavorable in terms of the stability requirements of Lasker's first-feeding hypothesis. Examination of these data in relation to data on intensity of spawning, birthdate distributions (Methot 1981), and year-class survival (Mais 1981; Smith et al. 1981) might suitably test the wind turbulence hypothesis.

An alternate method would be to investigate the evolution (generation, maintenance, and destruction) of fine-scale food strata in the upper layers of the ocean by coupling existing state-of-the-art one-dimensional mixed layer models (e.g., Garwood 1977) with appropriate biological models (Steele 1977) to test the sensitivity (biological response) to different characterizations of atmospheric forcing and to different initial conditions. Substantial new field measurements of both physical and biological processes over an extended period of the spawning season would be required to initialize and verify the model predictions. A carefully designed physical/biological mixed layer model would complement existing laboratory and field programs, and offers a method to properly integrate the effects of wind-generated turbulence over a spawning season, thereby contributing to our understanding of the important linkages of physical processes to recruitment success of the northern anchovy.

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An automatic feeder for liquids and wet or dry solids

HOWARD A. JEMISON III and ANDREW E. DIZON
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96812

and

MICHAEL M. WALKER
Department of Zoology
University of Hawaii, Honolulu, Hawaii 96822

An inexpensive and simple, remote-control conveyor-belt feeder is described. The feeder handles liquids and wet or dry solids.

Research on the magnetic sensitivity of tunas often requires remote-control feeders. Unfortunately, captive tuna only eat pieces of fish or squid that cannot be delivered by most commercially available feeders.

The feeders used in our research must be inexpensive and simple, since our resources and engineering capabilities are limited. The conveyor-belt feeders of Haralson and Ralph (1966) and Martin (1974) provide a model, but the feeder design described here is simpler, less expensive, and unique in its ability to handle liquids or wet or dry solids.

THE FEEDER

The feeder (Figure 1) consists of a conveyor belt mounted on a wooden 2.5-m (8-ft) 2 x 4 in. board. A longitudinal, 1.5 cm (deep) x 3 cm (wide) slot is cut as a guide for the belt. The groove diameter of the pulleys at each end is equal to the remaining thickness of the 2 x 4 in. wooden mount.

The pulleys are the most critical and difficult parts to build (Figure 1). The bottom of each pulley's groove is slightly humped to keep the belt aligned and is also knurled to provide sufficient grip on the belt. No bearings are used, since the duty cycle is short and rotational speeds are slow. The belt is made from 1-in. wide Velcro[1] tape, which is prestretched before the final sizing and sewing.

The containers can be small cups or vials, with small complementary circles of Velcro cemented or epoxied to the bottom of each. Using Velcro tape for the belt and on the containers allows the containers to be removed and refilled, cleaned, or replaced.

At one end of the feeder are mounted two aluminum plates that extend 15 cm beyond the end of the 2 x 4 in. wooden mount (see Figure 1). The plates serve as brackets for mounting one pulley, as well as a light and a photocell. The mounting holes are slotted to adjust belt tension. The light and photocell are mounted so that the container completely empties its contents before interrupting the photocell. The inside surfaces of the brackets are spray painted with flat black paint and the light source is collimated to reduce the possibility of glare and reflections inadvertently tripping the photocell.

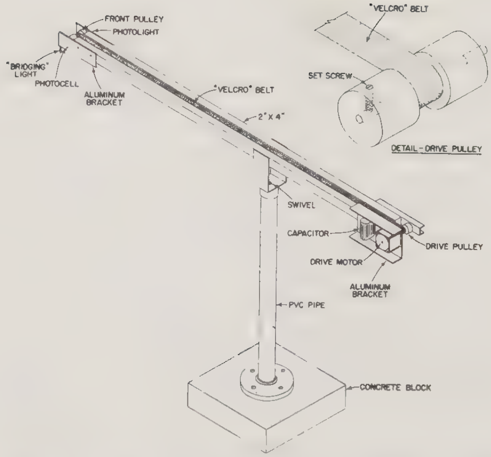

Figure 1. General view of feeder with a detail of the drive pulley.

On one side, at the opposite end of the feeder, is attached a larger bracket that serves as the mount for the motor and pulley. Since the opposite side need only hold the pulley, a 2.5-cm aluminum channel is sufficient. A 22-rpm, 3.5-cm-N (35-in.-oz), capacitor-start ac motor is connected directly to the pulley through the mounting plate. The feeder is mounted on a stand near its center of balance, and the stand is constructed so the feeder can be swung away from the tank for loading.

A "bridging" signal light is incorporated at the end of each feeder to alert the fish that a reward is forthcoming and to indicate to us the status of each feeder. This small ac light is placed in parallel with the ac motor on the outside of the photocell bracket. The light and motor turn on each time the feeder is activated.

Both control circuits are laid out and directly etched on one single-sided printed circuit (PC) board for simplicity (Figure 2, Detail A). The controller board and a 5-V 1.5-A power supply are mounted in a 20 x 20 x 20 cm aluminum enclosure. The PC board is mated with an edge connector for easy removal.

As shown on the block diagram in Figure 2, Detail B, a switch closure from a pushbutton or a computer-actuated relay applies a dc voltage to the controller, generating a digital pulse to turn the feeder on. This

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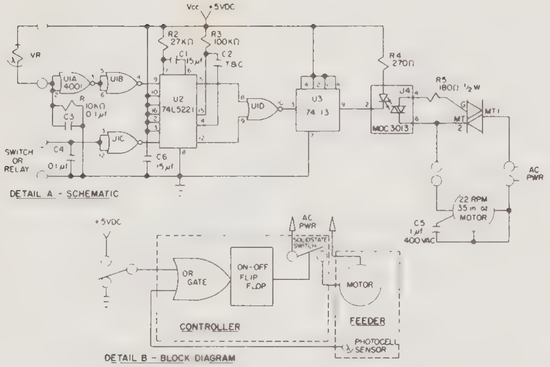
Vcc +5VDC
R2 27KΩ
R3 100KΩ
C1 15μf
C2 T&C
VR
U1A 4001
U1B
R 10KΩ
C3 0.1μf
U2 74LS221
U1D
U3 74 13
R4 270Ω
R5 180Ω ½W
J4
MOC 3013
G
MT1
MT 2
U1C
SWITCH OR RELAY
C4 0.1μf
C6 15μf
AC PWR
22 RPM 35 in oz MOTOR
C5 1μf 400VAC
DETAIL A - SCHEMATIC
+5VDC
AC PWR
SOLIDSTATE SWITCH
OR GATE
ON-OFF FLIP FLOP
MOTOR
CONTROLLER
FEEDER
PHOTOCELL SENSOR
DETAIL B - BLOCK DIAGRAM

Figure 2. (A) Schematic diagram of the feeder controller circuit. (B) Circuit block diagram.

rotates a container around the end pulley, emptying its contents and interrupting a photocell. The controller, sensing the interrupt, stops the feeder. The input to the controller can also accept a TTL or CMOS pulse for initiating a cycle.

The load capacity is dependent upon the length of the 2 x 4 in. board and the container size. Our feeders use 2-cm-diam vials with a 5-cc capacity and hold approximately 50 vials. The containers can be of any shape, and different shapes and sizes can be used simultaneously.

Further details are available on request.

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NOTE

1. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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RAPID AND SPONTANEOUS MATURATION, OVULATION, AND SPAWNING OF OVA BY NEWLY CAPTURED SKIPJACK TUNA, *KATSUWONUS PELAMIS*

This study was designed to test a hypothesis, formulated on the basis of preliminary observations, that skipjack tuna, *Katsuwonus pelamis*, captured in Hawaiian waters during their breeding season and maintained alive would ovulate spontaneously within a few hours after capture. If such did occur, and on a consistent and predictable basis, this would be of practical value in attempts to spawn these fish in captivity.

Methods

These investigations took place at the Kewalo Research Facility of the National Marine Fisheries Service Honolulu Laboratory. Six deliveries of live skipjack tuna were received from two commercial fishing vessels during June and July 1980, within the normal spawning season of the species in Hawaiian waters (Brock 1954; Matsumoto 1966). The fish had been caught by standard pole-and-line methods and transported to the receiving dock of the laboratory in baitwells. Upon delivery they were transferred to circular tanks, 7.3 m diameter by 1.1 m deep, provided with continuous flow of seawater. Time of capture for all groups was between 1500 and 1700; time elapsed between capture and delivery to the laboratory ranged from 3.5 to 8 h, with a mean of 5.5 h. Sea temperatures at the capture sites were not measured, but were probably between 25° and 30°C. Water temperatures in the holding tanks were about 25° to 26°C. With all except the first group, a siphon and straining net were used to sample water continuously from the holding tanks to detect the release of their slightly buoyant, pelagic ova. For the last four of the six groups, we arranged also to receive specimens fished from the same school but refrigerated on ice immediately after capture. All the specimens were between 40 and 50 cm in fork length (FL) and 1.4 to 2.2 kg; tunas larger than this are difficult to keep alive in the baitwells of these vessels (about 145 by 165 by 130 cm deep on the vessel which delivered five of the six groups). Skipjack tuna of this size are between 1 and 2 yr old and are probably in their first spawning season (Brock 1954; Yoshida 1971).

We determined gonadal maturation states of specimens at various specified times following their capture, either through biopsies on live specimens or through postmortem dissections. Unless a specimen is already running ripe, neither its sex nor gonadal maturity can be determined through external appearances. Biopsies involved extraction of gonadal tissue by catheterization through the urogenital pore of restrained, unanesthetized fish. Ova were teased free from unpreserved, fresh or refrigerated ovarian tissue, immersed in a 0.9% saline solution, and the diameters of 25 from each of the largest and second largest developing groups were measured with an ocular micrometer. Also, since we were interested primarily in the occurrence and progress of ovulation, we classified females into the following four categories: Unovulated—ripe ova not present in ovarian lumen, developing ova enclosed within follicles; ovulating—some ripe ova present in ovarian lumen but not easily stripped from females, follicles contain large, preovulatory ova 0.80 to 1.0 mm in diameter; ripe—ovarian lumen filled with large quantities of ova which can be easily stripped from females; spent—few residual ova present in ovarian lumen, follicles with relatively small ova of <0.5 mm diameter.

Results

Responses of each sex remained constant among the six groups. Testes of males sacrificed after 7 to 8.5 h appeared identical to those sacrificed and refrigerated on capture. All males had testes that were mature. white, and firm and had thick, viscous milt in the sperm ducts. None yielded milt when moderate stripping pressure was applied. To fertilize ova stripped from females, we had to squeeze milt directly from testes dissected from sacrificed males.

Observations on all six groups of female skipjack tuna received from 8 June to 31 July are summarized in Table 1. None of the 16 specimens killed and refrigerated on capture was in an ovulatory state. The maturing ova in the largest modal group averaged 0.59 to 0.64 mm in 14 of these females and 0.74 mm in another, while the remaining individual had relatively immature ovaries (Table 2). Nine females which died in transit to the laboratory were placed in refrigeration. Times of death had not been recorded by the fishing crews, but were <5 h after capture in all cases. None of these females had yet ovulated, and the ova in their largest developing modal groups averaged from 0.60 to 0.93 mm in diame-

TABLE 1.—Ovulatory status of skipjack tuna at different times following capture during June and July 1980.

Time	No.	Unovulated	Ovulating	Ripe	Spent
Refrigerated immediately after capture	16	16	0	0	0
Captive females, 0-5 h after capture[1]	9	9	0	0	0
Captive females, 5-6 h after capture	13	1	12	0	0
Captive females, 7-8.5 h after capture	12	3	1	8	0
Captive females, 15-65 h after capture	20	1	0	0	19

[1] Refrigerated after dying in transit to the laboratory; individual times of death not known, but <5 h after capture in all cases.

TABLE 2.—Mean sizes (mm)[1] of ova in largest and second largest modal group of developing ova in skipjack tuna killed and refrigerated immediately after capture, or refrigerated after dying in transit to the laboratory.

	Refrigerated on capture			Died in transit			
Date	No.	Largest group	Second group	No.	Time (h)[2]	Largest group	Second group
15 July	4	0.62	Not measured				
		0.61	Not measured				
		0.59	Not measured				
		0.60	Not measured				
21 July	7	0.60	0.42				
		0.60	0.39				
		0.60	0.40				
		0.59	0.41				
		0.59	0.40				
		0.60	0.39				
		0.59	0.40				
22 July	3	0.22	0.10	7	<4.5	0.84	0.44
		0.64	0.41			0.93	0.43
		0.74	0.44			0.76	0.44
						0.69	0.44
						0.72	0.42
						0.70	0.42
						0.72	0.45
31 July	2	0.62	0.41	2	<5	0.67	0.41
		0.62	0.43			0.60	0.41

[1] Standard deviations 0.02-0.04.

[2] Time between capture and death.

ter (Table 2). Of those kept alive, all but 1 of the 13 specimens examined 5 to 6 h after capture were ovulating but not yet ripe, while 8 of 12 examined after 7 to 8.5 h were ripe. Such ripe individuals yielded about 100,000 to over 150,000 ova when stripped. All but 1 of the 20 specimens examined 15 to 65 h after capture were spent. On all five occasions when the holding tanks were monitored for the presence of spawned ova, large numbers of ova were evident by the morning following delivery.

These observations clearly demonstrated that female skipjack tuna caught and kept alive during this time of year rapidly underwent the final stages of ovarian maturation and then ovulated ripe ova into the ovarian lumen. This response could be completed within 8 h after capture and occurred even in females that were so seriously traumatized that they died within a few hours after this time. Unless manually stripped, the ripe females released ova into the holding tank, and by the next day, 15 to 24 h after capture, were in a spent condition. Spawning behavior was not observed to occur. Instead, their behavior was invariably abnormal, as is typical for skipjack tuna during their first days in captivity, with individuals swimming aimlessly about the holding tanks.

The ovulated ova, both those released spontaneously into the tanks and those stripped from ripe females, were normal in size and appearance. They were spherical, transparent, averaged about 1.0 mm in diameter, and had a single oil globule about 0.24 mm in diameter. The fertilization rate of ova stripped from females about 8 h following their capture was only about 40% to 50%; this may reflect the quality of the ova or the small amounts of viscous milt squeezed from the dissected testes. The embryos hatched in about 30 to 31 h at 25° to 26°C and started feeding on the third day after hatching. Although they fed actively on rotifers, *Brachionus* sp., and copepod nauplii, we were not able to rear any beyond the 12th day.

Numerous investigators have described the multimodal size distribution of developing ova in the ovaries of maturing tunas. All of the ova in the most advanced modal group (about 0.60 mm or larger in these specimens) appeared to undergo final maturation and ovulation during this response but the second largest modal group seemed not to be affected. Ovaries from "control" specimens killed and refrigerated on capture and from those that died within 5 h contained an advanced modal group of maturing ova, as previously described, and a second, smaller modal group in which the ova averaged between 0.39 and 0.44 mm in diameter (Table 2). Ovaries from fully ovulated, ripe females and from recently spent females contained a residual modal group of similar, unovulated ova that averaged 0.39 to 0.49 mm in diameter (Table 3). These latter observations support the common assumption that in species with multimodal size distributions of developing ova, only the most advanced modal group will mature and be ovulated for a given spawning.

TABLE 3.—Mean sizes (mm)[1] of ova in largest modal group of unovulated ova in ripe or recently spent skipjack tuna.

Date	Hours after capture	Status	Ova diameter
28 June	8	Ripe	0.46
	8	Ripe	0.46
17 July	46	Spent	0.43
	46	Spent	0.40
21 July	7	Ripe	0.43
22 July	20.5	Spent	0.42
	25	Spent	0.39
23 July	[2]32-39	Spent	0.40
	32-39	Spent	0.43
	32-39	Spent	0.49
31 July	[2]6.5-15	Spent	0.45

[1] Standard deviations 0.02-0.04.

[2] Found dead in holding tanks, time interval since last seen alive.

Discussion

This rapid ovarian maturation, ovulation, and spawning appears to be a unique response to capture not previously reported. The trigger to this response is not known but appears related to stresses associated with capture and confinement. Witschi and Chang (1959) earlier concluded that ovulation of vertebrates could be facilitated by stress, but there has been a lack of direct evidence to support this conclusion. Indirect evidence for such a relationship within teleosts is suggested by ovulatory responses of certain species to treatment with corticosteroids (Hirose 1976; Sundararaj and Goswami 1977) and with epinephrine (Jalabert 1976), both of which have been reported to increase rapidly in serum concentrations following such stresses as handling and increased temperature (Mazeaud et al. 1977; Strange et al. 1977; Cook et al. 1980). The handling associated with being hooked, transported in crowded baitwells, transferred to shore tanks, and confined is obviously stressful and often fatal to newly captured skipjack tuna. Thermal stress may occur when they are confined in warm surface waters and prevented from returning to cooler depths after feeding.

Many additional aspects of this postcapture ovulatory response are not yet understood. Several aspects would be of particular interest: 1) the state of ovarian maturation that would be prerequisite for rapid egg development in females; 2) the seasonal availability of responsive females; 3) whether the time to complete ovulation, about 7 to 8 h in this study, will vary depending on such factors as water temperature, ovarian maturation, or time of day the fish are caught; and 4) whether this apparent response to acute stress is entirely an artificially produced anomaly, or whether it does have some relation to their natural spawning biology.

Past efforts to rear tunas in captivity (briefly reviewed by Kaya et al. 1981) had not heretofore resulted in dependable spawning procedures for any species. However, the occurrence and predictability of the ovulatory response to capture have now been applied to establish a routine procedure for spawning skipjack tuna at the Kewalo Research Facility. Additional spawnings have thus been accomplished during the summer of 1981, the second season of trials, and the response has been observed also in a second species of tuna—kawakawa, *Euthynnus affinis*. It would be of interest to determine whether other species will undergo a similar response to stresses of capture and confinement.

Acknowledgments

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CALVIN M. KAYA

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, HI 96812
Present address: *Department of Biology*
Montana State University
Bozeman, MT 59717

ANDREW E. DIZON
SHARON D. HENDRIX
THOMAS K. KAZAMA
MARTINA K. K. QUEENTH

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, HI 96812

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The need for satellite ocean color measurements in fisheries research and related activities

R. Michael Laurs
National Marine Fisheries Service
P.O. Box 271, La Jolla, California 92038

Abstract

Ocean color measurements from satellites have tremendous potential applications for use in fisheries research, and in the proper management of fishery resources.

Introduction

Ocean color measurements from space platforms may be used in living marine resource applications for quantitative determinations of ocean color that are directly related to chlorophyll and sestonic concentrations, the location of ocean fronts, effluents and circulation features and the detection of water masses.

Why ocean color is needed in fisheries

The application of satellite derived ocean color data in fisheries fall into categories related to fisheries research and management uses and the utilization in fisheries-aids products for use by commercial and recreational fishermen and other users in the fishing community.

Examples of the types of studies in the first category where satellite measurements of ocean color can be important include: 1) Year class strength and recruitment investigations where information is required on marine habitat characteristics, e.g., phytoplankton distribution, critical in the survival of early life stages of fishes. 2) Migration studies of highly mobile species such as tunas and billfishes and marine mammals where migration patterns are linked to ocean features, such as color boundaries which may be monitored over vast areas remotely from space. 3) Fishery forecasting efforts which utilize ocean color distribution to predict stock availability. 4) Fish stock assessment studies where models incorporate oceanographic/environmental conditions. 5) Fishery/pollution interaction and impact investigations showing waste disposal sites through color imagery. 6) Energy budget/ecosystems modelling approaches for estimating potential fish stock production. 7) Fisheries related habitat management where quantitative environmental information is required, e.g., changes in wetland use as detected and quantified by color imagery. 8) Marine mammal ecosystem studies. 9) Field studies where ocean color data are received in quasi-real time by scientists at sea for use in planning research operations and extrapolating in time and space the point source measurement made aboard ship.

In the second category the primary use of satellite ocean color measurements is to identify ocean areas where conditions may be favorable for concentrating fish. This can reduce search efforts to locate harvestable marine resources and thereby significantly reduce costs.

What ocean color data are needed

In fisheries research and fisheries management applications several types of ocean color products are needed including quantitative information on the distribution of chlorophyll, and of other bands of color, on diffuse attenuation (turbidity) and on the distribution of ocean color boundaries based on the ratio of various combinations of the color bands. Ocean color information needed to produce fisheries-aids products includes the locations of color boundaries and distribution of ocean color signatures and the diffuse attenuation coefficient (turbidity).

Preprocessing ocean color data

For fisheries research and fisheries management applications, in addition to removal of atmospheric contamination, ocean color data should be geographically rectified, cloud and land areas masked and areas of sun glint corrected and/or identified. To produce fisheries-aid charts interpretive symbols and/or narrative descriptions will be required. Also the ocean color information may be used in conjunction with other information, e.g., locations of thermal boundaries, sea surface temperature isotherm distribution, swell and wave information, etc.

Data format

For fisheries research and management applications, the data format will vary according to the specific requirements of individual experiments and investigations. The data may be required in computer compatible tapes, analog photographs or charts and in some cases may be received directly from the satellite at local receiving stations. In the latter case standard software packages for all preprocessing algorithms should be available for use at the receiving station or other processing facility. The data format for the fisheries-aids products will almost always be in chart form.

Spatial and Temporal Coverage

U.S. fishery needs for ocean color measurements are primarily in the coastal waters within the 200 mile economic zone surrounding the continental U.S., islands and territories; mid-ocean regions where important U.S. distant water fisheries are located; mid-ocean regions through which highly migratory fishes pass during migration to coastal waters where U.S. fisheries take place; and in mid-ocean regions important in marine mammal research and protection. There is also a lesser need for global coverage. The frequency of coverage will vary depending on location and perhaps to some extent on season. Generally 2-day coverage will be required in coastal/local waters and 3 to 5 day coverage for most mid-ocean applications. Global coverage may be needed on the order of every 15 to 30 days.

The acceptable time delay from the time of satellite overpass to delivery for fisheries applications will vary from near-real time to several days.

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ESTIMATING AND MONITORING INCIDENTAL DOLPHIN MORTALITY IN THE EASTERN TROPICAL PACIFIC TUNA PURSE SEINE FISHERY

Each year the purse seine fishery for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific is responsible for the incidental kill of thousands of small cetaceans,[1] primarily dolphins or "porpoise." Yellowfin tuna are often associated with small cetaceans in this region and fishermen have used this association since 1959 to catch tuna (McNeely 1961; Perrin 1969; Fox 1978). During the purse seining operation, cetaceans encircled with yellowfin tuna by the net may become entangled and accidentally drown. In such cases, the fishermen retain the tuna and discard the cetaceans at sea.

The Marine Mammal Protection Act of 1972 requires the tuna fishery to be managed so that the dolphin populations are maintained at specific population levels and that incidental mortality be reduced to insignificant levels. The National Marine Fisheries Service (NMFS) has the responsibility of monitoring the dolphin mortality and of assessing the impact of dolphin mortality on dolphin populations. NMFS carries out research on the abundance and distribution of dolphins, their biology, the level of incidental mortality, and methods for reducing incidental mortality.

Beginning in 1971, the NMFS regularly placed observers on purse seiners to collect data on the incidental mortality of dolphins. Prior to 1974, however, only a few observers were hired to collect data; the amount of data collected, therefore, is too small to produce a precise estimate of total incidental mortality. Most estimates from this period place the total at about 300,000 to 500,000 animals/yr. Estimates for 1974 and 1975, which are more precise, are 140,000 and 157,000 animals killed, respectively, for the U.S. fleet (Smith[2]).

After a U.S. District Court ruling in 1976, the NMFS set an annual quota of 78,000 animals for

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[1] Dolphin, in this paper, is used as a general term referring to all small cetaceans impacted in the fishery. Mortality or kill refers to dolphin mortality incidental to the catch of yellowfin tuna. The unit of fishing effort "set" is defined as a single deployment of a purse seine net around an aggregation of dolphin or tuna. Tuna catches are expressed in the unit short tons, as it is the most common form in which these statistics are reported.

[2] Smith, T. D. Report of the status of porpoise stock workshop. Southwest Fish. Cent. Adm. Rep. LJ-79-41, 120 p.

1976 as the maximum allowable kill by the U.S. tuna fishery. Methods for monitoring the mortality levels, and projecting when the quota would be reached during the year, were required. A yellowfin tuna quota (175,000-195,000 short tons) managed by the Inter-American Tropical Tuna Commission (IATTC), around which the tuna fishermen planned their fishing operations, was also in effect and had to be incorporated into the procedure. In this paper, we describe statistical methods which have been used to estimate the annual incidental dolphin mortality for the U.S. fleet during the year and at the end of the year since 1976. This estimative procedure has been used also for foreign fleets by IATTC since 1979 (Allen and Goldsmith 1981).

Methods

The data sources used to monitor and estimate incidental dolphin mortality were the scientific observer program of the NMFS and the logbook records of the IATTC.

The NMFS observer program provides data on discarded dolphins. Trained technicians were placed aboard a random sample of U.S. tuna vessels to collect data of various types, including number of dolphins killed in a set, amount of tuna caught, species of tuna, fishing location, vessel capacity, and duration of trip.

The IATTC maintains a logbook system whereby it collects data on type of set, fishing locations, tonnage of catch, species of tuna, vessel carrying capacity, and other information that are recorded in logbooks by fishermen.

Three mortality rates were used to estimate total dolphin mortality. They were obtained by dividing the total observed kill of dolphins by the total observed number of dolphin sets (kill-per-set), by the total observed number of days-at-sea (kill-per-day), and by the observed total catch of yellowfin tuna associated with dolphin (kill-per-ton).

Estimation Procedures

Three estimation procedures were used in this study. The first procedure was based on kill-per-day statistics to monitor the dolphin mortality during the year; the second was based on kill-per-ton combined with kill-per-day to project the closure date; and the third was based on kill-per-set to estimate the total mortality at the end of the year.

The kill-per-day and the kill-per-set methods were based on stratified ratio estimators. Trips from which the dolphin set data were taken, were stratified according to fishing locality, vessel carrying capacity, yellowfin tuna catch, gear type, and fishing time. The fishing locality and time were directly related to the IATTC's yellowfin tuna regulatory system, which includes 1) an annual quota on yellowfin tuna catch within the Commission's yellowfin regulatory area (CYRA) (Fig. 1), 2) season closure to enforce the quota on yellowfin tuna catch, and 3) a "last trip" allocated at season closure to each vessel that fished during the open period (Table 1).

Kill-Per-Day Method

The kill-per-day method requires all trips to be stratified according to gear type, vessel carrying capacity, and fishing time; this method was developed to monitor kill during the season. The year was divided into three periods, each designating a trip type. Trip-type 1 included all vessel

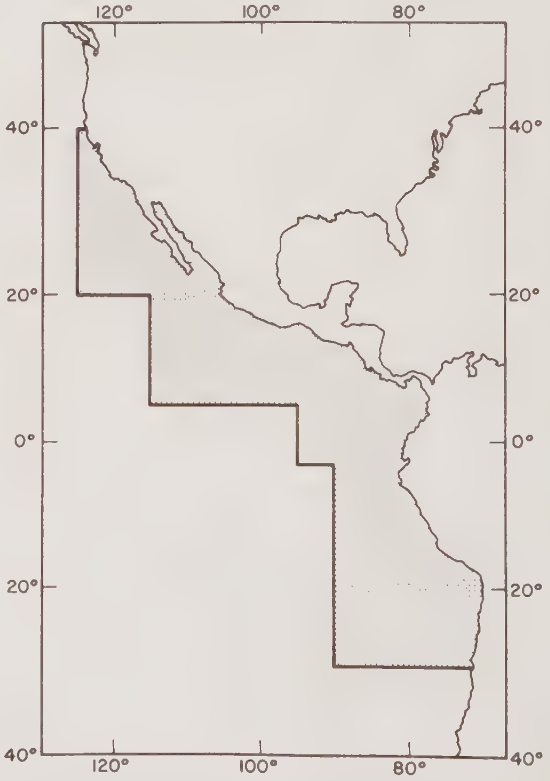

FIGURE 1.—The major part of the Inter-American Tropical Tuna Commission Yellowfin Regulatory Area (Courtesy of IATTC).

days through the IATTC season closure date (1 January through 26 March); trip-type 2 included all vessel days approximately corresponding to the "last trip" (27 March through 4 July); and trip-type 3 contained all vessel days after 4 July. This stratification of time was used to preclude overlapping trips. When a trip crossed a stratum boundary, it was assigned to more than one stratum. For example, for a trip lasting from 1 March to 5 May, the days from 1 March to 26 March would be assigned to trip-type 1, and days from 27 March to 5 May assigned to trip-type 2 (Table 1).

TABLE 1.—Layout of stratification of vessel trips (sets) for kill-per-day and kill-per-set methods.

Kill-per-day method with maximum 30 strata: 15 for each gear type

NMFS vessel class	Trip 1 1 Jan.-26 Mar.	Trip 2 27 Mar.-4 July		Trip 3 5 July-end of fishing	
		open[1]	regulated	open[2]	regulated
I					
II					
III					

Kill-per-set method with maximum 32 strata

IATTC vessel class	Successful sets		Unsuccessful sets	
	Inside CYRA	Outside CYRA	Inside CYRA	Outside CYRA
1				
2				
3				
4				
5				
6				
7				
8				

[1] Trips not subject to IATTC season closure. Most of them were "last trips."

[2] "Last trips" or trips made outside of CYRA.

The statistical formulation for dolphin mortality estimation according to a stratified ratio estimator is as follows (Cochran 1977):

For the ith stratum, $i = 1, \ldots, I$,

let N_i = total number of vessel trips

n_i = number of observed trips

X_{ij} = kill for the jth observed trip $j = 1, \ldots, n_i$

Y_{ij} = days-at-sea for the jth observed trip

r_i = kill-per-day

s_{r_i} = the approximate sample standard error of r_i (kill-per-day)

M_i = total number of days-at-sea

$\hat{T}_i$ = estimated total kill

then
$$r_i = \frac{\sum_j X_{ij}}{\sum_j Y_{ij}} \qquad (1)$$

$$s_{r_i}^2 = \frac{N_i - n_i}{N_i} \, \frac{r_i^2}{n_i} \left(\frac{s_x^2}{\overline{X}_i^2} + \frac{s_y^2}{\overline{Y}_i^2} - 2 \, \frac{\operatorname{cov}(X,Y)}{\overline{X}_i \, \overline{Y}_i} \right)$$

where
$$s_x^2 = \frac{\sum_j (X_{ij} - \overline{X}_i)^2}{n_i - 1}$$

$$s_y^2 = \frac{\sum_j (Y_{ij} - \overline{Y}_i)^2}{n_i - 1}$$

and

$$\operatorname{cov}(X,Y) = \frac{\sum_j (X_{ij} - \overline{X}_i)(Y_{ij} - \overline{Y}_i)}{n_i - 1}$$

$$\hat{T}_i = r_i M_i$$

$$\hat{T} = (\Sigma \hat{T}_i) = \Sigma r_i M_i$$

$$s_{\hat{T}}^2 = \Sigma M_i^2 \, s_{r_i}^2 .$$

The ratio estimator (r_i) and its approximate sample variance ($s_{r_i}^2$) are unbiased only under certain conditions (Cochran 1977). Alternative variance formulas have been suggested to correct the bias (Royall and Eberhardt 1975; Royall and Cumberland 1981). We chose the commonly used variance formula ($s_{r_i}^2$) in our procedure because the results of a simulation study showed that the bias of the ratio estimator and the approximate variance is negligible (Lo[3]). The simulation study was based upon the empirical dolphin mortality data collected in 1977.

Beginning on 30 June 1976, NMFS observers radioed their mortality counts to a shore base each month (starting in 1977, estimates were made biweekly). Data from this source were used to estimate cumulative mortality and to project the date when the annual quota would be reached.

Combined Kill-Per-Day and Kill-Per-Ton Method

The method using combined kill-per-day and kill-per-ton was developed to project at the end of each month the date on which the quota would be reached. It included two procedural steps:

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[3] Lo, N. C. H. Simulated results of a commonly used ratio estimator applied to incidental dolphin mortality by U.S. tuna purse seiners in the eastern tropical Pacific. Manusc. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

1. A series of cumulative dolphin mortality estimates for each future month was made by summing the current total mortality, based on kill-per-day statistics, and the projected mortality for future months, based on kill-per-ton statistics.

To calculate the projected cumulative mortality in future month m, we denote, at the end of month h,

$\hat{T}_h$ = the estimated current total mortality from the observed data by kill-per-day method
$\hat{T}_{m,h}$ = the projected cumulative mortality at the end of month m based upon T_h
U_m = the tonnage of yellowfin tuna catch in month m
$\hat{U}_m$ = the historical monthly tonnage average of yellowfin tuna catch
Z_W = observed kill-per-ton weighted by number of vessels of two gear types.

We then have

$$\hat{T}_{m,h} = \hat{T}_{m-1,h} + U_m \cdot Z_W \doteq \hat{T}_{m-1,h} + \hat{U}_m Z_W$$

$$= \hat{T}_h + \left(\sum_{i=h+1}^{m} \hat{U}_i\right) Z_W$$

for $m = h+1, h+2, \ldots, 12 \quad 1 \leq h \leq 11$

and $s_{\hat{T}_{m,h}}^2 \doteq s_{\hat{T}_h}^2 + \left(\sum_{i=h+1}^{m} \hat{U}_i\right)^2 s_{Z_W}^2 + Z_W^2 \sum_{i=h+1}^{m} s_i^2$

where s_i^2 is the sample variance of yellowfin tuna catch for month i, and h refers to the month when the up-to-date total mortality was estimated, with the assumption that cov $(Z_W, \Sigma U_i)$ and cov (U_i, U_j) for $i \neq j$ are negligible. $s_{\hat{T}_{m,h}}^2$ is an approximate sample variance of $T_{m,h}$ by the Delta method (Seber 1973). $s_{Z_W}^2$ is the variance of weighted kill-per-ton. Z_W and $s_{Z_W}^2$ are based on the formulas of the ratio estimator (Equation (1)).

2. For quota Q, the projection of closure date was calculated as follows. If $Q < \hat{T}_{12,h}$, the month g was chosen where $\hat{T}_{g-1,h} < Q < \hat{T}_{g,h}$. The projected date ($V$) in month g was then obtained as:

$$V = \frac{Q - \hat{T}_{g-1,h}}{\hat{T}_{g,h} - \hat{T}_{g-1,h}} \cdot V_g$$

$$= \frac{Q - \left(\hat{T}_h + Z_W \sum_{i=h+1}^{g-1} \hat{U}_i\right)}{\hat{U}_g \cdot \hat{Z}_W} \cdot V_g$$

where V_g is the number of days in month g.

Kill-Per-Set Method

The kill-per-set method was developed to estimate the annual mortality at the end of the year. It requires that all dolphin sets be stratified in three ways: tonnage of yellowfin tuna catch during dolphin set, vessel carrying capacity, and fishing location (Table 1). Time of the year was not a separate factor as it correlated closely with fishing location.

The kill-per-set method was formulated in the same manner as the kill-per-day method (Equation (1)), except the auxiliary variable Y_{ij}'s were observed sets, r_i was kill-per-set, and M_i was total number of sets. In addition, the estimated total dolphin mortality was corrected for nonreporting in IATTC logbooks, inside and outside the CYRA, by a factor C, where C is the ratio of tonnage of yellowfin tuna taken with dolphin which were landed and weighed at port, to the tonnage of yellowfin tuna recorded in the logbooks as an estimate at sea. The mortality for strata without observed data was estimated with the kill-per-set of adjacent vessel-class strata. The resulting sample statistics are in Table 2.

TABLE 2.—Sample statistics[1] of kill-per-set method for 1976 U.S. purse seine tuna fleet.

IATTC vessel class	Inside CYRA			Outside CYRA		
	r_i	$S^2_{r_i}$	$X\,(n_i)$	r_i	$S^2_{r_i}$	$X_i(n_i)$
Successful sets:						
1	—	—	—	—	—	—
2	4.00	—	1(1)	—	—	—
3	—	—	—	—	—	—
4	3.02	2.17	68(5)	13.60	41.94	88(4)
5	7.08	4.42	37(4)	43.90	277.76	62(4)
6	10.60	15.51	44(4)	26.70	—	6(1)
7	17.60	7.72	148(1)	12.90	26.58	140(12)
8	22.00	19.62	32(2)	1.00	—	1(1)
Unsuccessful sets:						
1	—	—	—	—	—	—
2	0	—	1(1)	—	—	—
3	—	—	—	—	—	—
4	4.59	12.70	22(6)	9.90	22.95	10(3)
5	0.90	0.15	20(5)	4.50	8.24	8(2)
6	16.40	320.16	14(5)	8.31	27.91	—
7	3.15	0.28	20(4)	12.10	107.27	8(5)
8	3.27	7.78	22(2)	0	—	1(1)

[1] r_i = kill-per-set, $S^2_{r_i}$ = sample variance of r_i, X_i = number of observed dolphin sets, n_i = number of observed trips.

Results

The estimated mortality based on the kill-per-day method for each of the three periods was 24,000 animals (SE = 5,400) (1 January-26 March), 29,000 animals (SE = 5,300) (27 March-4 July), and 53,000 animals (SE = 21,000) (5 July-end of fishing), to give a total kill of 105,000 animals (SE = 22,000) for 1976 (Table 3).

Using the kill-per-set method, we computed dolphin mortality estimates adjusted for nonreporting of sets inside and outside the CYRA (Table 4). The estimated total dolphin mortality with this method was 104,000 animals (SE = 13,000).

The closure dates for reaching the quota of 78,000 animals as projected at the end of June, July, and September were in October. The fishery itself, however, was not actually closed until November, after a court hearing process.

The annual quotas for 1977, 1978, and 1979 were 52,000, 42,000, and 31,000 animals, respectively, and the mortality was monitored biweekly by species/stock. Due to the improvement and use of rescue techniques by the fishermen and the motivation of tuna fishermen to reduce dolphin mortality, the kill-per-day estimates of most of the species/stock have been below their annual quotas. The kill-per-set estimate for annual total dolphin mortality by U.S. seiners for 1977, 1978, and 1979 was 24,000 (SE = 3,500), 19,000 (SE = 3,700) and 18,000 animals (SE = 2,200), respectively.

Discussion

Procedures for estimating dolphin mortality have used the basic models tailored to suit the existing conditions of the fishery and available monitoring resources since 1976. The number of strata for the kill-per-day method has been reduced because only vessel classes II and III are fishing tuna with dolphin (the majority being class III vessels), and all the vessels are required to use a standard gear, i.e., super apron. Moreover, since 1979, there has been no quota on the yellowfin tuna catch. Thus, the entire year is "open" for fishing (Table 1).

The kill-per-set method is more precise than the kill-per-day method because the standard error is smaller. However, in order to make during-the-year estimates, procedures to collect accurate information on the number of dolphin sets for the whole fleet at regular intervals during the year, yet need to be developed. Analysis of use of the kill-per-set method indicated that the number of vessel classes (eight) was unnecessarily large. A revision of the stratification scheme for this method is currently in progress.

The statistical techniques of monitoring and estimating dolphin mortality can be applied to other kinds of incidental catches. The 1976 dolphin mortality data, in particular, demonstrated the complexity of the situation where the selection of auxiliary variables for ratio estimator and the stratification of data to reduce the variance were not straight forward. These factors have to be taken into account to ensure high precision of the estimates.

TABLE 3.—Estimated kill by U.S. vessels in 1976 using kill-per-day method.

	1 Jan.-26 Mar		27 Mar.-4 July		5 July-end of fishing		1 Jan.-end of fishing	
Gear type	Kill	SE	Kill	SE	Kill	SE	Kill	SE
Conventional	23,769	5,448	24,884	5,316	47,068	20,531	95,721	21,896
Experimental	144	—	3,764	440	5,727	1,931	9,635	1,980
Total	23,913	5,448	28,648	5,334	52,795	20,622	105,356	21,985

TABLE 4.—Estimated kill by U.S. vessels in 1976 corrected for nonreported sets (SE in parentheses) using kill-per-set method.

Area	Tons YF on dolphin landed[1]	Tons YF on dolphin logged[1]	Correction factor C Column 2 ÷ column 3	Adjusted kill
CYRA	55,112	47,180	1.17	44,061 (4,424)
Outside	70,745	65,248	1.08	55,801 (12,690)
Total				99,862 (13,439)
Experimental and chartered vessels				4,211 (—)
Grand total				104,073 (13,439)

[1] IATTC record

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NANCY C. H. LO

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
La Jolla, CA 92038

JOSEPH E. POWERS

Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA
Miami, FL 33149

BRUCE E. WAHLEN

Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
La Jolla, CA 92038

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A FISHERIES VIEW OF THE DRAIN

by R. Bruce MacFarlane

Discharging saline irrigation water in the Chipps Island area has definite environmental implications. This area already experiences increased salinity resulting from diversions of fresh water to the San Joaquin Valley and Southern California. Further increases in salinity from the drain may significantly impair the biological communities dependent upon this area. This is a critical habitat for oceanic fishes that enter fresh water to breed, particularly striped bass. For example, changing salinity patterns can alter the composition and abundance of prey species resulting in reduced production of striped bass, a fish already suffering substantial decline. Additionally, the effectiveness of man-made marshes in purifying wastewater is in initial stages of testing and is still questionable.

Projections of environmental impact are largely the results of mathematical models. The Delta-Suisun Bay is a highly complex system. Modeling such a system is difficult and in many cases not justified by current knowledge and understanding. Model results must be interpreted with caution and cannot be accepted as definitive. Estimates of concentrations of substances in the drain water vary widely from report to report, casting more doubt on the validity of model forecasts. (Compare, for example, estimates in the Interagency Drainage Program — IDP — report to those in the Draft Supplemental Environmental Impact Statement for the San Luis Unit.) Concentrations alone, without knowledge of the volume of drainage discharge and the rate of flow of receiving waters, are not very useful in assessing likely effects. The IDP report on the San Joaquin Valley Master Drain projects eventual discharges amounting to 22% of the total water flowing into the San Francisco Bay system. If municipal sewage discharges are added in, then 32% of the "fresh water" entering the Bay will be of degraded quality. This certainly suggests that biological impacts will not be negligible.

Reservations regarding projections of the impact of additional nitrogen are certainly justified, especially in the case of shallows, where potential for explosive growth of algae is high. However, the impact of added heavy metals and pesticides must also be looked at critically. The National Marine Fisheries Services (NMFS) at Tiburon has considerable evidence that present levels are adversely affecting abundance and health of striped bass in the area. Projections of concentrations of heavy metals and pesticides reveal that many will exceed background levels and government standards. IDP's conclusion that the discharge would not be toxic clearly misunderstands the intent of water-quality criteria and disregards the possibility of accumulation of toxins by organisms. These reflect current knowledge of what will protect the health and welfare of aquatic organisms and humans.

Implementation of this drainage plan seems premature. There are too many questionable assumptions and unresolved problems with potentially serious consequences for this alternative to be considered acceptable. The NMFS is on record as favoring evaporation ponds to dispose of saline, subsurface drainage water. The NMFS also favors alternatives that would reduce demand for more surface water for irrigation, thereby reducing salt accumulation in soils. These alternatives would include water-pricing reform, water conservation (including more efficient irrigation techniques), groundwater management, and selection of crops more compatible with environmental conditions, such as higher salt tolerance or lower water requirements.

FOR FURTHER READING

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INSTRUMENTS AND METHODS

Temporal and spatial resolution of pump sampling systems

D. L. Mackas* and R. W. Owen†

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Abstract—A simple empirical method is described for determining the fine-scale resolution of continuous flow-through sampling systems. An input delta function is provided by injection of fluorescent dye into the sampler intake. The output fluorescent signal provides time-domain estimates of delay and signal spread; Fourier transformation of the output provides the frequency domain transfer function of the system. Systems with direct intakes (hose or through-hull fitting) can resolve features of 30-s duration or less; however, sea chest intakes cause substantial blurring of the input signal. Attempts to increase vertical spatial resolution by slow lowering rates can result in profiles characterized by apparent micropatchiness and multiple layering, artifacts of the procedure.

INTRODUCTION

Continuous flow sensors are now widely used to sample spatial and temporal distributions in aquatic environments. Variables measured include temperature, salinity, chlorophyll fluorescence, dissolved nutrients, and particle abundance (Lorenzen, 1966; Kelley, Whitledge and Dugdale, 1975; Steele and Henderson, 1977; Pugh, 1978; Denman and Mackas, 1978). The primary motivation for continuous sampling is the potential for much finer resolution than can be achieved by discrete sampling methods. In particular, the understanding of small-scale features and processes (e.g., plankton patchiness, fronts, and vertical layering) is almost totally dependent on the resolution, accuracy, and interpretability of continuous measurements.

Although the useful sample density obtainable from flow-through sensors is large, it is finite. Optimum resolution and analytical efficiency are achieved only by an appropriate matching of digitizing interval, instrument response time(s), rate of movement of the sampler intake, and scales of spatial and temporal variability of the quantity being mapped. Both slow instrument response and mixing of sample water in the supply plumbing (if present) attenuate high-frequency components of the data and give a smoothed time series relative to the sampled system. Such attentuation has both beneficial and adverse effects. On the positive side, it allows slightly longer intervals between digitizing of the incoming data (see the discussion of aliasing in Platt and Denman, 1975). Conversely, measurement at scales

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* Institute of Ocean Sciences, Sidney, B.C. V8L 4B2, Canada.
† Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, CA 92038, U.S.A.

overlapping into the zone of attentuation may be essential for many applications; the smoothed output data will then result in underestimation of small-scale gradients and, if the data are eventually expressed in spectral form, will impose an artificial truncation of the high frequency or high wavenumber end of the estimated variance spectrum.

In this article we describe a method for measuring the effective cut-off frequency of a flow-through sampling system and present data and response spectra for several pump systems. We then show how the time-scale cut-off can impose severe constraints on both spatial and temporal sampling of rapidly varying data. We also show that published examples of vertical micro-patchiness (e.g., STRICKLAND, 1968) may be artifacts resulting from internal wave displacements past a slowly descending sample intake.

METHODS

Calculation of response spectra and selection of input signals

Except that the relevant time scales are substantially longer, the analysis is exactly equivalent to that conventionally applied to linear electronic systems. JENKINS and WATTS (1968) provided a development from which we extract the following important points:

The output $u(t)$ of a 'physically realizable' system can be expressed as a weighted integration over all prior inputs

$$y(t) = \int_0^\infty h(u) x(t-u)\,\mathrm{d}u, \tag{1}$$

where $x(t)$ is the input function and $h(u)$ is the weighting coefficient at time lag u. [The only constraint is that $h(u)$ must not itself vary significantly during the measurement.] The complex frequency spectrum of the output is $Y(f)$ and is the Fourier transform of the output series

$$Y(f) = \int_{-\infty}^{\infty} y(t) \mathrm{e}^{-i2\pi ft}\,\mathrm{d}t, \tag{2}$$

where f is a frequency expressed in cycles per unit time. The output spectrum is also equal to the product of the spectra of input and weighting functions

$$Y(f) = H(f) \cdot X(f), \tag{3}$$

where

$$H(f) = \int_0^\infty h(u)\,\mathrm{e}^{-i2\pi fu}\,\mathrm{d}u \tag{4}$$

and

$$X(f) = \int_{-\infty}^{\infty} x(t)\,\mathrm{e}^{-i2\pi ft}\,\mathrm{d}t. \tag{5}$$

The 'power spectrum' $|Y(f)|^2$ is the squared modulus of $Y(f)$ [i.e., if $Y(f)\,a\cos(f) + ib\sin(f)$ then $|Y(f)|^2 = a^2 + b^2$]. It partitions the variance of the time series $Y(t)$ among the contributing frequency scales [see JENKINS and WATTS (1968) or PLATT and DENMAN (1975) for more detailed development and for equivalent equations corresponding to finite series length and discrete sampling intervals]. Because the expected frequency dependence of the power spectrum can be derived for stochastic processes such as turbulent diffusion, data on oceanographic distributions are commonly reduced to this form (PLATT and DENMAN, 1975).

For our purposes, the input function $x(t)$ is the data field being sampled (one realization of a random process), $|X(f)|^2$ is the power spectrum we would like to estimate (assumed to be statistically representative of the random process under study), $y(t)$ is the output observed from the instrument, and $|Y(f)|^2$ is the corresponding observed power spectrum. Finally, $H(f)$ is the combined transfer function of the sampling system plumbing and the sensing instrument, and $|H(f)|^2$ is the squared gain function, relating the magnitude of the output variance to the magnitude of the input variance within each frequency band. Conveniently, an input function which is a 'spike' at one sampling point and zero elsewhere (an impulse or delta function), has a power spectrum that is constant with frequency. The output time series resulting from this input is equal to a constant multiple of the time domain weighting function $h(u)$ plus a small (one hopes) measurement error $e(t)$. The output power spectrum $|Y(f)|^2$ is proportional to the squared gain spectrum plus the noise spectrum due to instrument drift, jitter, and quantizing error.

$$|Y(f)|^2 = |H(f)|^2 \cdot |X(f)|^2 + |\varepsilon(f)|^2, \tag{6}$$

where $|\varepsilon(f)|^2$ is the noise power spectrum and can be estimated from the output spectrum of a constant (or better, a slowly and linearly varying) input. The estimated 'true' spectrum is therefore

$$|X(f)|^2 = \frac{|Y(f)|^2}{|H(f)|^2} - |\varepsilon(f)|^2. \tag{7}$$

In practice, both $Y(f)$ and $H(f)$ normally become small relative to $\varepsilon(f)$ at large f and the usefulness of a reconstructed input spectrum is questionable.

If the input spike is sufficiently strong to make the measurement error $e(t)$ very small relative to the output signal $y(t)$, the input and output series can be treated as deterministic functions rather than as realizations of random processes. The ensemble or frequency band averaging conventionally applied in spectral analysis of random data is therefore unnecessary, and the transfer function can be estimated to sufficient accuracy directly from the discrete Fourier transform of the digitized output signal. Many computer programs are available for this task; we used the Waveform Analysis Pac available for the Hewlett–Packard HP-85 desk-top computer.

Sampling system—sensors and water supply

The data and analyses reported here correspond to five different but reasonably typical flow-through sampling configurations. In each, the final component is a portable instrument package (MACKAS, LOUTTIT and AUSTIN, 1980) consisting of a bubble trap, a resistive particle counter, a Turner Designs fluorometer, and an Applied Microsystems Ltd. temperature and conductivity sensor (all connected in series). For convenience of measurement and because it has the slowest response time of the various sensors, we used the output signal from the fluorometer for our analyses. The 'impulse' input function was a syringe of fluorescent dye (a dilute solution of Rhodamine B in seawater), which a SCUBA diver injected quickly (<1 s) into the initial seawater intake. The total system response was invariably slow relative to the manufacturer-specified (and observed) time constant of the fluorometer, implying that the observed high-frequency attentuation was dominated by mixing within the supply system. On this basis, we have accepted the system plus fluorometer gain function as a slightly conservative but adequate model for all sensors in the system. Other applications might require independent evaluation for each of several sensors (for example, an AutoAnalyzer® might have both longer lag time and considerably greater internal smoothing of the sample signal). Output of the fluorometer was recorded continuously on a paper strip chart from which the data were digitized at time intervals short relative to the rate of output signal variation (range 2 to 30 s, depending on the supply system).

Five different supply plumbing configurations (A to E) were examined. System A is used for vertical profiling and consists of a submerged intake hose (35 m long, 3.25 cm i.d.), a deck mounted Moyno progressive cavity pump, and 20 m of 2 cm i.d. hose leading to the instrument package. The pump output is 1.25 l s^{-1}, of which 25% is passed through the sensors and the remainder discharged overboard. B to E are the scientific seawater supply systems on four local research vessels and are used for horizontal mapping of near-surface distributions. The pump intake for E lies within a recessed sea chest (vol. 2 m^3), which also provides cooling water for the ship's engines. The outer wall of the sea chest is a flush-mounted grating of about 50% porosity, and the dye spike was injected through this grating. Although the ship was stationary during the test, its engines were run in neutral at cruising speed to approximate normal flow rates through the sea chest. The remaining systems (B, C, and D) have direct intake through the hull. B and C have relatively short runs (10 to 15 m) of internal supply piping, while D has a run of nearly 40 m. All of the ships' systems provided flows of 0.19 to 0.25 l s^{-1} to the sensor package.

RESULTS

Time domain representation of sampling system resolution

Output time series for the various pump-and-plumbing systems are shown in Fig. 1a to e. Two estimates of signal modification are presented in the figure. Delay is the mean lag time in seconds for arrival of the fluorescent tracer and is given by:

$$\text{Delay} = \frac{\sum_{i-1}^{N} F_i i \Delta t}{\sum_{i=1}^{N} F_i}, \tag{8}$$

where F_i is the fluorescence of the ith digitized point, Δt is the digitizing interval in seconds, and N is the number of sampling intervals from dye injection to final disappearance of the output pulse. This Delay statistic will normally be equal to the mean residence time of water in the system (system volume divided by flow rate) provided the tracer moves with the flow so that there is no chromatographic separation of tracer and carrier. The appropriate use of this statistic is to align the data output with the record of sample location. FWHA (full width at half amplitude) is a measure of the broadening of the <1-s input pulse and is the time between upward and downward crossings of $F_i = 0.5\ F_{\text{max}}$. This is an estimate of the temporal resolution (as opposed to the phase shift) imposed by the sampling system and is also useful as a guide to the sampling frequency needed to avoid possible aliasing errors.

The following features should be noted from the figure: First, although Delay and FWHA are obviously correlated, the correlation is imperfect and their numerical values are con-

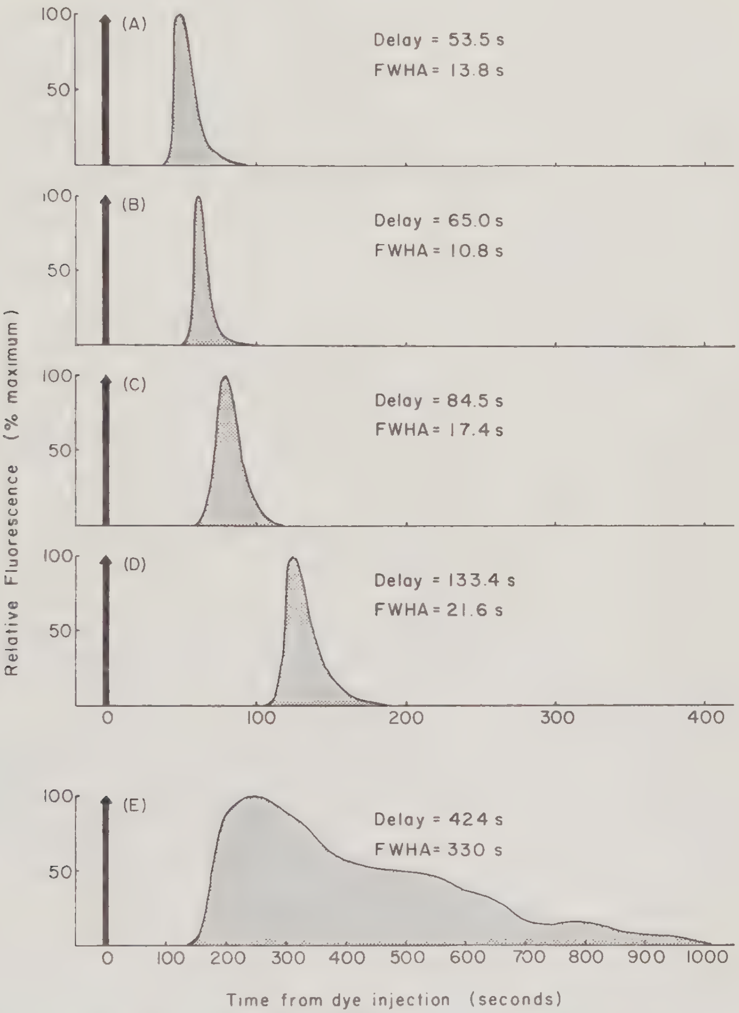

Fig. 1. Input (arrow) and output (stippled) signals for injection of fluorescent dye into five pump sampling systems. A is a vertical profiling system, B to D are ships' seawater supplies with direct intakes through the hull, and E (note scale change along time axis) is a ship's supply with intake drawing from a semi-enclosed sea chest. See text for details and definition of Delay and FWHA statistics.

siderably different; FWHA is normally much smaller than Delay. Information will therefore be lost from the output signal if the data logging interval is set to match the mean residence time of the system (a fairly common practice, see e.g., STEELE and HENDERSON, 1977). Second, the output is characteristically skewed, with mean delay time being longer than the delay to $F_i = F_{\max}$. Third, system E (sample drawn from the sea chest) has delay and pulse width that are extremely large compared to the other systems. In addition, there are indications with this system of multiple decaying output pulses (possibly caused by a slow rotational circulation within the sea chest).

Frequency domain representation of sampling system resolution

Fourier transformation of the output signals from the various sampling systems gives the power spectra shown in Fig. 2. The spectra have been normalized to a maximum value of unity at the lowest frequency band. The effect of this normalization is to depict the squared gain function for each system; an 'observed' power spectrum calculated from a data series will be the within-frequency-band product between the 'true' spectrum (specifically that for a single realization from the underlying random process) and the squared gain spectrum of the system used to collect the data.

The optimum form for the above gain spectrum is rectangular; unity for all frequencies below the Nyquist frequency $(2\Delta t)^{-1}$ and zero for all higher frequencies. However, the measured spectra all show a more gradual transition into a roll-off region in which the squared gain varies approximately as the inverse square of frequency. In system E the roll-off commences at very low frequencies indicating strong attenuation of variability at all scales shorter than about 10^3 s (the spectral peak at 0.003 cycles s^{-1} represents the periodicity of the multiple output pulses mentioned in the previous section). The remaining four sampling systems are much more similar in their spectra and are characterized by higher corner frequencies and more rapid and uniform roll-off. The half-power points fall at time scales (cycle lengths) of 54.1, 40.8, 68.5, and 90.9 s for systems A to D, respectively. These time scales are approximately four times the corresponding FWHA estimates and are extremely well correlated with them ($r^2 = 0.996$ vs 0.836 for the correlation with Delay). To a good approximation, a discrete sampling interval roughly equal to the FWHA time scale both eliminates potential aliasing and records nearly all of the information passed by the sampling system. The investigator can use these data in their raw recorded form but should note that both time and frequency domain data have been attenuated at the shortest time scales included in the analysis. Alternately, the investigator can resort to a more elaborate procedure of digitally filtering the data to give a more rectangular frequency response function and a better match between corner and the final effective sampling frequencies (see e.g., Bendat and Piersol, 1971).

Implications for spatial resolution

The most common application of continuous flow sensors lies in sampling of spatial variation rather than purely temporal variation. For studies of near-surface horizontal variability, the sampler intake is towed from or attached to a ship moving at a speed of 2 to 10 knots (roughly 1 to 5 m s^{-1}). Systems A to D all show good resolution of features having greater than about 30-s duration; their equivalent spatial resolution (at easily obtained ship's speeds) can therefore be set between 30 and 150 m, which is adequate for many purposes. (A more severe limitation is usually found at the other end of the sampling scale, i.e., the maximum distance a ship can travel within a time scale that can reasonably be described as synoptic.) Somewhat finer spatial resolution can be obtained by reducing in size or eliminating the bubble trap (vol. 10 l), but smaller scales are in general more effectively sampled by *in situ* sensors. In contrast, the spatial scale for system E is 0.65 to 3.4 km, which would be too coarse for description of sharp and frequently encountered gradients such as frontal boundaries.

Pump sampling systems can impose more severe restrictions when used for studies of vertical distributions. Vertical gradients in the ocean are substantially stronger than horizontal gradients; significant changes in concentration often occur over vertical distances of 1 to 5 m or less. This suggests that resolution of such features is best achieved by lowering the sample

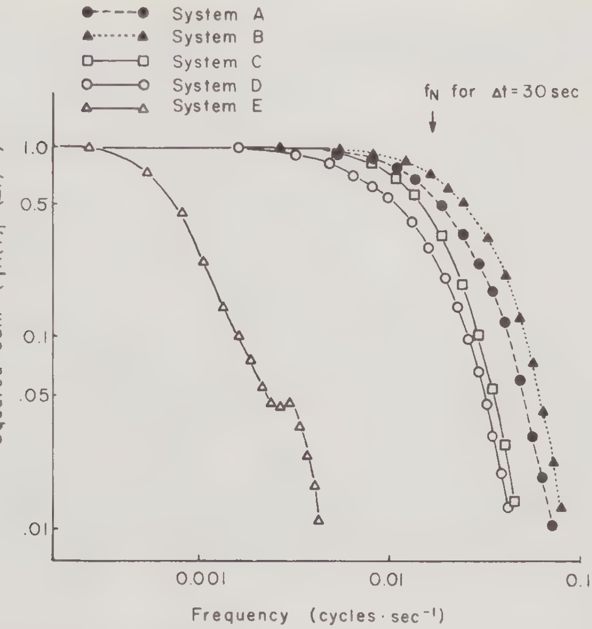

Fig. 2. Squared gain spectra (output variance vs frequency) for the five sampling systems. Small arrow labelled f_N indicates the maximum frequency detected by a 30-s discrete sampling interval.

intake slowly (e.g., 1 to 2 m min^{-1} or slower). However, as noted by HOLLIGAN (1978), this is potentially misleading because the vertical structure can experience internal wave or turbulent displacements that are substantially more rapid than 1 m min^{-1}, and the desired ‘snapshot’ can easily become a ‘multiple exposure’.

To illustrate the above problem, we present simulated results of slow vertical profiling through a water column perturbed by internal gravity waves. The internal wave displacement is modeled as a solitary wave in a two-layer fluid with the lower layer substantially thicker than the upper (BENJAMIN, 1966). Input parameters are selected to approximate water properties and wave amplitudes observed off La Jolla, California (LAFOND and COX, 1962; MULLIN and BROOKS, 1972). The vertical distribution of chlorophyll is simulated by superposition of a Gaussian chlorophyll maximum centered on the pycnocline, a nearly uniform upper layer concentration, and an asymptotic approach to zero below the pycnocline. Equations for the profile are:

$$\mathrm{Chl}(\eta) = A + B\mathrm{e}^{-(\eta-P)^2/s^2} \quad \text{for} \quad \eta \leqslant P \tag{9}$$

and

$$\mathrm{Chl}(\eta) = A\mathrm{e}^{-C(\eta-P)} + B\mathrm{e}^{-(\eta-P)^2/S^2} \quad \text{for} \quad \eta > P, \tag{10}$$

where η is the depth at which the sampled stratum would be in the absence of internal wave displacement and is calculated from the sampling depth $Z(t)$ and the displacement $F(\eta, t)$; P is the pycnocline depth (also in the undisturbed water column); and $A = 2.5$, $B = 5$, $S = 3$, and $C = 0.25$ are constants respectively determining the upper layer concentration, the concentration within and vertical thickness of the sub-surface maximum, and the exponential rate of decrease of concentration below the pycnocline. Figure 3 shows a time vs depth section of the displacement of vertical structure caused by passage of the internal wave, and three possible sampling trajectories through the structure (1 m min^{-1} lowering speed through an unperturbed water column, 1 m min^{-1} intersecting the wave trough, and 4 m min^{-1} intersecting the wave trough). Figure 4 a to c shows the corresponding simulated profiles of chlorophyll concentration. Samples from a non-wavy region (Fig. 4a) accurately portray the estimated chlorophyll distribution. However, in the presence of even a solitary internal wave, the sampler may sample the same water two or more times at different depths (Fig. 3; see also Pingree, Holligan and Head, 1977; Haury, Briscoe and Orr, 1979). This produces (Fig. 4b) an apparent chlorophyll profile characterized by spurious fine-scale peaks and troughs. The exact profile (number and intensity of the apparent peaks) depends on the interaction between lowering rate; starting time of the profile; phase, speed, and amplitude of the wave(s); and width and location of the chlorophyll maximum. However, the simulated profiles bear a disturbing resemblance to the multiple-peaked fluorometric profiles reported by Strickland (1968) off La Jolla. These and similar profiles (e.g., Berman, 1972; Kiefer and Austin, 1974; Kiefer and Lasker, 1975) have been interpreted as evidence for fine-scale vertical patchiness that is missed by conventional sampling with water bottles at standard depths. Although such an interpretation is at least partially valid in that to produce such highly structured profiles there must be a narrow stratum with markedly higher (or lower)

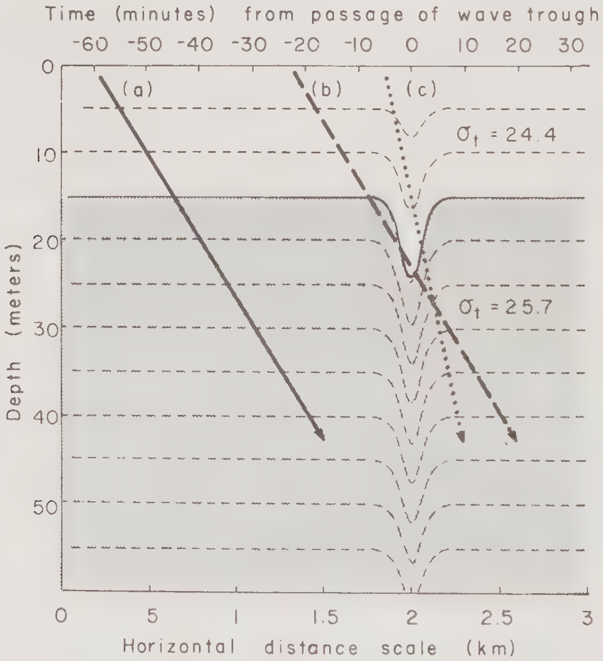

Fig. 3. Simulated internal wave displacements in a two-layer water column. Upper layer is 15 m thick when undisturbed and has density corresponding to water of 18°, 33.8×10^{-3} salinity. Lower layer extends to bottom at 120 m and has density corresponding to 12°C, 33.8×10^{-3}. Wave amplitude is 10 m at the interface and wave speed is 0.51 m s^{-1}. Dashed lines indicate the variation of displacement trajectories as a function of depth. Three sampling trajectories through the wave structure are shown. Solid line a is 1 m min^{-1} lowering speed through an undisturbed water column. Broken line b is 1 m min^{-1} intersecting the trough. Dotted line C is 4 m min^{-1} intersecting the trough.

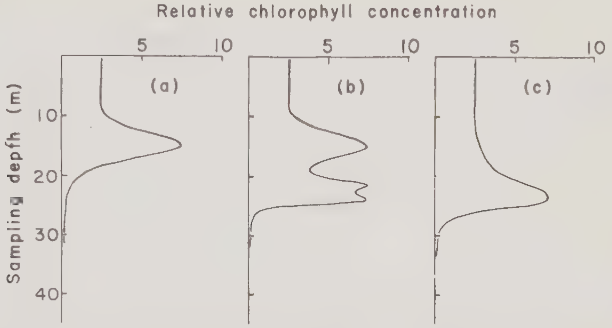

Fig. 4. (a, b, c) Simulated chlorophyll profiles for the three sampling trajectories shown in Fig. 3. See text for equations describing the form of the undistorted profile.

chlorophyll concentration, the multiple layering may be entirely an artifact of the sampling procedure. We suggest two procedural options for eliminating this possible artifact from studies of vertical microdistribution. One is to make the sampling more synoptic. This can be done either by using a specialized microsampler to obtain simultaneous discrete samples at closely spaced depths (Owen, 1981), by rapid lowering of a fast-response *in situ* sensor (if available), or by greatly increasing the lowering rate of the pump intake (and engineering a reduced FWHA time scale to maintain the needed spatial resolution). Figure 4c shows the more accurate profile obtained within the wave trough using a four-fold increase in simulated lowering rate. A second option is to include as part of the pump profiling system sensors for physical variables (temperature, conductivity, and from these salinity and density). If correction is made for temperature offset produced within the sampling system, an independent 'fast' profile of the physical structure (e.g., by a concurrent CTD cast) can then be used to define a density vs depth chart onto which the remaining pump profile variables can be plotted (Denman and Herman, 1978; Mackas, Boyd, Smith and Santander, 1981). This approach has the added advantage that the upper cut-off frequency for internal wave perturbations can be estimated from the data, and the lowering rate altered to suit individual sampling locations. Distortion of the profile will normally be minimal if the lowering rate is set to be greater than about twice the product of the buoyancy frequency (converted to cycles per unit time) and the local wave amplitude (usually 10 to 20 m or less for relatively high frequency and near-surface internal waves).

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A Comparative Study of Fish Yields from Various Tropical Ecosystems

GERALD G. MARTEN
Environment and Policy Institute
East-West Center
Honolulu, Hawaii 96848

AND

JEFFREY J. POLOVINA
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96812

MARTEN, G.G. AND J.J. POLOVINA. 1982. A comparative study of fish yields from various tropical ecosystems, p. 255-289. *In* Pauly, D. and G.I. Murphy (eds.) Theory and management of tropical fisheries. ICLARM Conference Proceedings 9, 360 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.

Abstract

There is an immense variation in actual and potential fish yields, both within and between different kinds of aquatic tropical ecosystems. The finfish catches from lakes, reservoirs, rivers, continental shelves and coral reefs all fall in approximately the same range of 0.1 to 30 tonnes/km^2/year, with most catches falling in the range of 1 to 10 tonnes/km^2/year and modal values falling in a range of 3 to 6 tonnes/km^2/year. The yields from estuaries and ponds can be considerably higher (up to 120 tonnes/km^2/year without supplementary feeding), and the yields from open ocean are considerably lower (.002 to .05 tonnes/km^2/year). Within the tropics, the best physical indicator of a fishery's potential yield is water depth, and the best biological indicator is primary productivity. Some ecosystems such as rivers, estuaries and ponds have relatively high fish yields for their primary productivity, presumably because of organic matter inputs. Other ecosystems such as coral reefs and open oceans have relatively low fish yields, presumably because of long food chains. However, no single indicator, including primary productivity, can predict fish yields very precisely. More refined yield assessments will have to be empirical in nature, recognizing the importance of fishing practices in assessing potential yields and giving particular attention to how the composition of fish communities in different habitats is altered by fishing and other human activities.

Introduction

There is an immense variation in fish yields in different parts of the tropics. The annual yield from a square kilometer of intensively managed fishponds can be as much as a million times the average annual fish catch from a square kilometer in the middle of the ocean. Even fisheries which are not intensely managed can vary by a factor of more than ten thousand in their yields, depending upon where they are located and the ecological conditions that prevail.

Sufficient information has accumulated on these fisheries to attempt an assessment of why they vary so much. This review examines the extent to which different fish yields are associated with different aquatic ecosystems such as lakes, reservoirs, rivers, estuaries, continental shelves, coral reefs and open ocean. Also, this review examines the extent to which fish yields can be explained by biological or physical characteristics of the different ecosystems and how these characteristics differ from one ecosystem to another.

One of the motivations for such an assessment is to assist inventories of the potential of tropical fisheries. Because it has not been feasible to conduct stock assessments and establish commercial catch record systems of the sort desired for management in all of the numerous lakes, rivers, estuaries, etc., that are situated in the tropics, there is a need for methods with limited data requirements to assess fishery potentials and the yield implications of present fisheries practices.

Methods

The basic information for this review comes from records of finfish yields (wet weight) in various ecosystems throughout the tropics. The analysis is not precise because the information is not precise. Large errors can be expected in fish yield statistics for a variety of reasons, many deriving from the artisanal character of multispecies tropical fisheries. One of the weakest points is the estimation of fishing effort, which is important to yield estimates because such estimates are customarily made by multiplying catch per unit effort (from a sampling of fish landings) by the total effort in the fishery. It can be extremely difficult, however, to know the effort of a fishery that consists of thousands of individual fishermen operating out of canoes along a complex shoreline where transportation and communications may be poor or non-existent. This may be further complicated if a fishery has restrictive regulations which encourage the fishermen to avoid reporting their catch faithfully.

It is important to appreciate the spatial scale of the yield estimates, which most often are highly aggregated. A single number may be used to represent the yield from a lake whose fishery production is ten times as great in its shallow inshore areas as its offshore areas. The estimate for a river may embrace both the highly productive flood plains and relatively sterile headwaters. The estimate for a coral reef fishery may cover an area that is a patchwork of highly productive coral and less productive sandy areas. Estimates from the open ocean come from areas that are thousands of square kilometers in extent and may be very heterogeneous.

The lower end of the scale of fish yields from each ecosystem is not well defined. The less productive fisheries, which by necessity have fewer fishermen, tend not to have catch records. In one sense the lower end of the scale is zero because there are places where each of the ecosystems is not fished at all. Even with regard to potential yield, the lower end of the scale is very low if the spatial scale is fine enough.

The upper end of the scale is reflected in maximum sustainable yields (MSYs). There are limitations in estimating the upper end of the scale because the MSY of a particular fishery can be inferred reliably only from actual yield experiences. However, in many instances none of the yields have been large enough to give suitable information concerning the maximum. This may be because the fishery has never been intensive enough to approach the maximum. The small-scale fisheries that are found on many tropical lakes and seashores are restricted to the inshore areas, so that offshore areas remain unexploited.

It may also be that the stocks have not been fished in the intricate fashion that would evoke the highest yield. This may involve the kinds of fishing gear that are used and the species of fish that are being harvested. Any history of yields, including the maximum from that history, is specific to a particular technology and may be considerably below the maximum possible yield.

Whenever possible, MSYs were estimated by tabulating the total annual finfish catches (summed over all species) for different years or different locations and plotting the catches against the fishing effort in those years or locations. In the absence of such information, the yields of fisheries with intensive fishing were considered to be representative of their MSY. It is possible that the yields of some of the intensely fished fisheries were depressed by overfishing, but we do not consider this to be a serious error because heavy fishing of a multispecies fishery does not usually result in significant reduction of the total catch, provided fishing activities do not lead to habitat destruction or other degradation of the resource base. Finally, in the absence of intensive fishing, MSY was estimated to be one-half the virgin biomass multiplied by natural mortality (when available).

Among indicators of potential yield, particular attention is given in this report to primary productivity because of its biological relationship to fish yield, and where possible we have tabulated fish yield and primary productivity figures from the same fisheries. The estimates are highly imprecise because of the spatial and seasonal variation in primary productivity, but the relationship seems to be strong enough to show through. For some ecosystems we did not find primary productivity and fish yield figures for the same fisheries. In those cases we assembled information on the range of primary productivities in the ecosystem in order to compare it with the range of fish yields.

Results

LAKES, RESERVOIRS AND PONDS

Table 1 lists a number of tropical lakes (primarily African) in order of their catch per unit area. There is a range of 0.1 to 23 t/km^2/year.

Toews and Griffith (1979) reported a significant negative correlation between fish catch per unit area and the size of African lakes. This relation is probably due in part to the fact that smaller lakes tend to have a higher percentage of shallow water, and shallow water generally has higher fish production than deep water. This is reflected in the observations of Kud-

Table 1. Fish yields from tropical lakes.

Lake	Location	Area (km^2)	Catch (t/km^2/yr)	Source
Upemba	Zaire	530	23	Henderson and Welcomme (1974)
Yercaud*	India	.08	22	Oglesby (1977)
Kyoga	Uganda	2,700	18	Henderson and Welcomme (1974)
George*	Uganda	250	15	Ganf (1975)
Mwadingusha	Zaire	393	13	Henderson and Welcomme (1974)
Malombe	Malawi	390	13	Henderson and Welcomme (1974)
Guiers	Benin	170	13	Henderson and Welcomme (1974)
Ooty*	India	0.34	10	Oglesby (1977)
Tanganyika* (north)	Tanzania	3,575	8.9	Mann and Ngomirakiza (1973)
Mweru	Zaire	4,580	6.8	Henderson and Welcomme (1974)
Edward	Uganda	2,300	6.8	Henderson and Welcomme (1974)
Victoria* (inshore)	Kenya	1,300	6.2	Melack (1976)
Chilwa	Mozambique	1,750	5.6	Henderson and Welcomme (1974)
Kodaikanal*	India	0.26	5.3	Oglesby (1977)
Rukwa	Tanzania	2,000	4.9	Henderson and Welcomme (1974)
Lanao*	Philippines	—	4.8	Frey (1969)
Chiuta	Mozambique	113	4.4	Henderson and Welcomme (1974)
Albert*	Uganda	5,600	4.2	Cadwalladr and Stoneman (1966)
Mweru-Wa-Ntipa	Zaire	1,520	3.8	Henderson and Welcomme (1974)
Kitangiri	Tanzania	1,200	3.4	Henderson and Welcomme (1974)
Baringo*	Kenya	160	3.3	Melack (1976)
Malawi (Southern portion)	Malawi	6,000	2.5	Turner (1977a, b)
Victoria* (offshore)	Kenya, Uganda, Tanzania	41,200	2.1	Kudhongania and Cordone (1974)
Chad*	Chad	16,000	1.4	Welcomme (1972a)
Bangweulu*	Zambia	2,733	1.3	Toews and Griffith (1979)
Tumba	Zaire	1,767	0.6	Henderson and Welcomme (1974)
Maji Ndombe	Kenya	1,300	0.5	Henderson and Welcomme (1974)
Rudolf	Kenya	7,200	0.3	Henderson and Welcomme (1974)
Kiru	Tanzania	2,699	0.1	Henderson and Welcomme (1974)

*Catch and primary productivity data also used in Fig. 3.

hongania and Cordone (1974) on Lake Victoria and Turner (1977a, b) on Lake Malawi that fish stocks are significantly larger in the shallow peripheral portions of the lake than they are in the deep, central area.

The main reason that shallow water has higher fish production is that primary productivity is higher in shallow water due to the availability and recycling of nutrients for photosynthesis. It is quite likely, however, that an even higher percentage of the primary production passes to fish in shallow water because of the more significant role of the benthic food chain. This is because plankton and detritus have a better chance of sinking to the bottom without being captured by the pelagic food chain if the water is shallow (see Jones, this vol.). Benthic food chains tend to be shorter than pelagic food chains because many benthic invertebrates which eat sediment are large enough to be fish food, whereas pelagic food chains start with microscopic organisms and pass through a series of progressively larger organisms before reaching a size sufficient for fish food. More of the primary production is translated to fish production when the food chain is short.

Small lakes also tend to be more productive because the nutrients and detritus which pass into them from outside can make a significant contribution to the lake's productive capacity in comparison with the biological production that originates in the lake itself. Finally, small lakes tend to be more intensively exploited, whereas the offshore areas of a large lake are not easily accessible to the small-scale fisheries which exploit them.

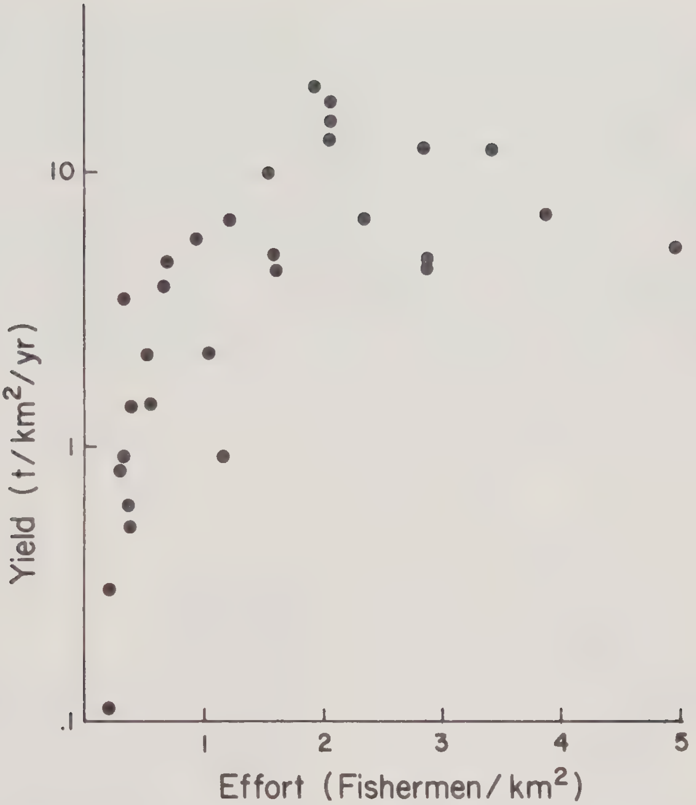

Fig. 1. Fish yields and fishing effort on African lakes (from Henderson and Welcomme 1974).

Although the yields in Table 1 vary by a factor of more than 100, the lower part of the range appears to correspond to lakes where the fishing intensity is not sufficient to yield a harvest near the maximum. Fig. 1 shows the relationship between fishing intensity (as measured by the number of fishermen per unit area) and catch per unit area for some African lakes. Since different lakes have different MSYs, it is not possible to infer the MSY simply as the maximum of the cluster of points in Fig. 1. However, Fig. 1 gives the impression that the range of MSYs may be approximately 1 to 23 t/km^2/year.

The main difference between reservoirs and lakes is that a reservoir was once a river or dry land before the river was dammed. As a consequence, a reservoir does not possess a full complement of lake fauna, even though the physical conditions of the reservoir are the same as those of a lake. This means that unless new fish are introduced, there may be parts of the reservoir that are virtually uninhabited by fish and their food, and the efficiency of translation of the reservoir's biological production to fish yields may be correspondingly reduced.

Fernando (1976) and Welcomme (1979) have reviewed the fish yields of reservoirs, and Table 2 lists the fish yields of some tropical reservoirs. The bottom end of the range is similar to that for lakes, but the upper end is 50% greater than for lakes. The upper end may be higher because many reservoirs can draw temporarily on the standing stock of trees and other plant materials which were inundated at the time the reservoir was formed. In addition, if the reservoir has an ecological vacuum, it is possible to introduce high-productivity fish such as the African cichlids and attain higher levels of production than would be possible with native fauna.

Henderson and Welcomme (1974) demonstrated a relationship between the morphoedaphic index (total dissolved solids/average depth) and fish yields in a series of African lakes. Although Fig. 2 shows a definite relationship between morphoedaphic index and yield, it is also apparent that most of the variation in yield is not explained by the morphoedaphic index.

Table 2. Fish yields from tropical reservoirs.

Reservoir	Country	Area km^2	Catch (t/ km^2/yr)	Source
Pacal	Indonesia	4	35	Sarnita (1976)
Pening	Indonesia	22	32	Sarnita (1976)
Dorma	Indonesia	4	28	Sarnita (1976)
Jombor	Indonesia	2	20	Sarnita (1976)
Lam praloung	Thailand	19	14	Chukajorn and Pawapootonan (1976)
Mwadingusha	Zaire	393	13	Henderson and Welcomme (1974)
Sirin thorn	Thailand	292	11	Chukajorn and Pawapootonan (1976)
Amaravathy*	India	9	11	Sreenivasan (1978)
Lam Poa	Thailand	230	11	Chukajorn and Pawapootonan (1976)
Sathanur*	India	13	10	Sreenivasan (1978)
Nzilo	Zaire	280	10	Henderson and Welcomme (1974)
Ayame	Ivory Coast	135	7.4	Henderson and Welcomme (1974)
Nam pung	Thailand	21	6.2	Chukajorn and Pawapootonan (1976)
Ubolratana	Thailand	410	6.0	Bhukuswan and Pholprasith (1976)
Prijetan	Indonesia	2	4.8	Sarnita (1976)
Volta*	Ghana	8,482	4.7	Henderson and Welcomme (1974)
Sentir	Indonesia	1	4.3	Sarnita (1976)
Kainji	Nigeria	1,270	4.2	Henderson and Welcomme (1974)
Kalen	Indonesia	1	4.0	Sarnita (1976)
Chulaporn	Thailand	12	3.3	Chukajorn and Pawapootonan (1976)
Tirumoorthy	India	5	2.8	Sreenivasan (1978)
Sandy Nulla	India	3	2.6	Sreenivasan (1978)
Stanley*	India	147	2.3	Sreenivasan (1978)
Lam takong	Thailand	44	2.2	Chukajorn and Pawapootonan (1976)
Jatiluhur	Indonesia	83	2.2	Sarnita (1976)
Nasser	Egypt	3,330	2.1	Henderson and Welcomme (1974)
Bhavanigasar*	India	79	2.0	Sreenivasan (1978)
Nam oon	Thailand	86	1.7	Chukajorn and Pawapootonan (1976)
Krishnagiri*	India	13	1.0	Sreenivasan (1978)
Kariba	Zambia	5,364	0.8	Henderson and Welcomme (1974)
Ghandi Sagar	India	660	0.7	Dubey and Chatterjee (1976)
Rihand	India	302	0.7	Natarajan (1976)
Nagaryanasagar	India	184	0.5	Natarajan (1976)
Konar	India	15	0.2	Natarajan (1976)
Tana	Kenya	3,500	0.1	Henderson and Welcomme (1974)

*Catch and primary productivity data also used in Fig. 3.

The morphoedaphic index has been reviewed by Ryder et al. (1974). The value of the morphoedaphic index for predicting fish yields presumably derives from its relationship with primary productivity. Total dissolved solids are related to the supply of nutrients required for primary production, and the depth of the water reflects the extent to which the nutrients are available at the lake surface where most of the primary production occurs. Of the two components of morphoedaphic index, depth is a better indicator of fish production than total dissolved solids (Matuszek 1978).

Melack (1976) and Oglesby (1977) have demonstrated a relationship between fish yields and primary productivity. We ran a multiple regression analysis of yield versus mean depth and primary productivity for the lakes and reservoirs in Table 3. The results indicated primary productivity to be a better predictor than depth. Comparing Fig. 3 with Fig. 2 suggests that primary productivity is also a better predictor of fish yields than the morphoedaphic index.

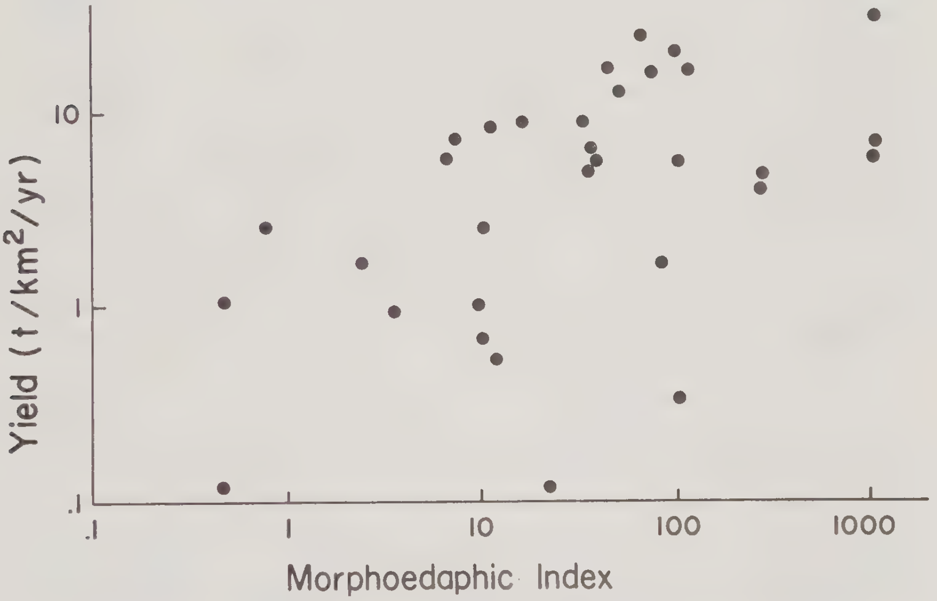

Fig. 2. Fish yields and morphoedaphic index (from Henderson and Welcomme 1974).

If a curve is put through the points in Fig. 3, it appears not to pass through the origin, suggesting that fish yields greater than zero are only possible once primary production exceeds a threshold. This would be expected from food-chain theory (Haussman 1971). There is also a suggestion of an upward curvature in Fig. 3, which implies that the efficiency of translation of primary production to fish production may be greater at higher levels of primary productivity. This may be because phytoplankton tend to be larger under highly productive conditions, requiring a shorter food chain (as particle size increases up the chain) in order to reach fish food size.

There is considerable variation in the fish yield (about fivefold) for any given level of primary productivity in Fig. 3. Part of the variation is undoubtedly due to errors in estimating yield and primary productivity, but it

Table 3. Physical and biological characteristics of some tropical lakes and reservoirs.

Lake	Primary productivity (gC/m^2/yr)	Depth (m)	Morphoedaphic index
George	1,500	2	83
Ooty	1,380	3	48-158
Amaravathy	1,175	12	4
Yercaud	1,060	2	55-100
Volta Res.	1,040	10	3
Tanganyika	1,040	330	2
Victoria (offshore)	1,000	63	2
Kainji	890	10	7
Albert	970	25	29
Volta	930	18	2
Victoria (inshore)	850	6	2
Bhavanigasar Res.	850	12	4-17
Stanley Res.	849	17	7-15
Sathanur	844	10	32-80
Krishnagiri Res.	565	5	47-108
Chad	370	4	103
Bangweulu	270	4	6
Baringo	200	7	83
Kodaikanal	160	2	14

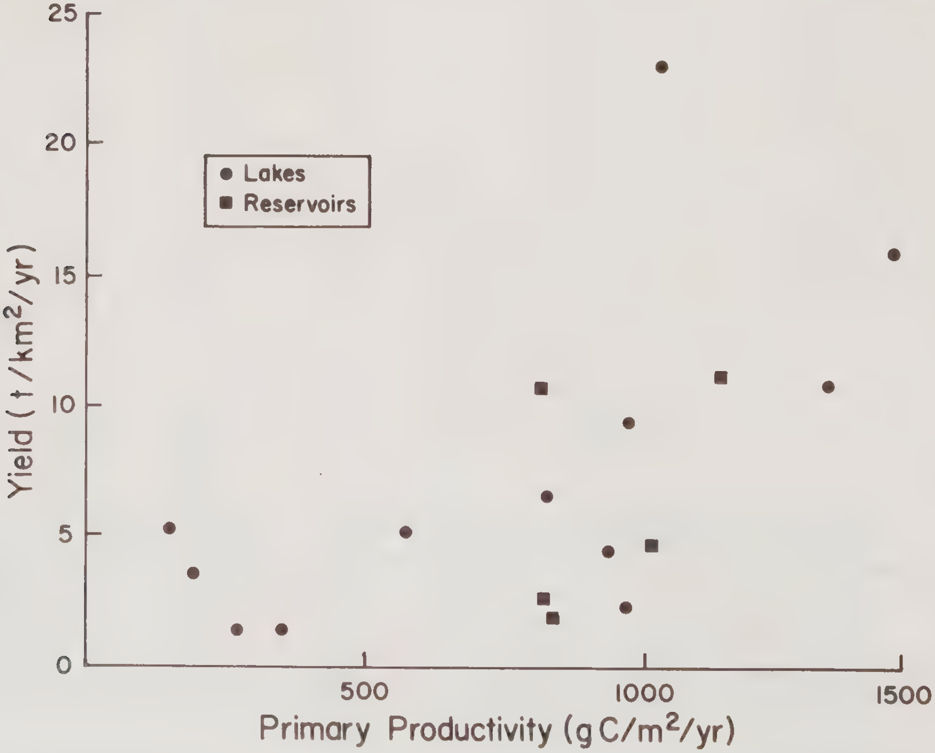

Fig. 3. Fish yields and primary productivity in tropical lakes and reservoirs, based upon lakes and reservoirs in Tables 1, 2 and 3 (r = .61).

appears the prediction would not be highly precise even in the absence of such errors. The loose relationship between primary productivity and fish yields is due in part to variation in the efficiency with which primary production is translated to fish yields. This may be due to the efficiency of the fishery (the fact that yield may be below MSY) or the efficiency with which primary production is converted to fish production through the food chain. Another limitation of primary productivity as a predictor is that the productivity of small lakes can derive in large measure from detritus and other organic materials that come from outside.

Oglesby (1977) explored other measures of the food available to fish as predictors of fish yield and found a closer correlation between yield and the standing crop of benthic fauna in temperate lakes. A similar relationship could have been sought for zooplankton and pelagic fish. The value of fish food abundance as a yield predictor may be limited, however, because the same standing stock of fish food could have a low or high production depending upon whether or not it is intensely harvested by the fish (Hayne and Ball 1956).

Fishponds, intensively managed with fertilization but without food supplementation, can show fish yields as high as 120 t/km^2/year (Bardach et al. 1972). This is partly due to the fact that the primary productivity of intensively managed ponds can be as much as three times the maximum primary productivity of lakes. It is also because fishponds can be stocked with fishes, such as carp and tilapias, which are highly efficient at translating primary production to yields. The yield from ponds can also be very high because they lack the predators which compete with fishermen for the fish harvest in natural water bodies such as lakes and rivers. The relationship between yield and primary productivity can be very close in fishponds (Fig. 4).

Rivers

Welcomme (1979) has reviewed the fisheries ecology of rivers. Table 4 lists the yields of some tropical rivers. Fig. 5 shows the relation between fish yields and the number of fishermen on some tropical rivers.

Rivers show a broader range of yields than lakes. The low end of the range in yields for rivers is lower than for lakes, and is associated with headwaters in areas of highly weathered soils which have a very low primary productivity and a correspondingly low fish production. The high end of the range for rivers is slightly higher than for lakes, even though the primary productivity of rivers is generally lower than that of lakes. The explanation may lie in the fact that rivers receive from the large watershed area that surrounds them a significant quantity of nutrients and organic material which contributes to the biological productivity of the fishery. Moreover, many of the rivers with high yields are flood-plain rivers that can draw upon the terrestrial productivity of the areas they flood, and the highest yields in Table 4 are probably due in large measure to the quantity of municipal sewage received by those rivers. Welcomme (1979) found the best predictor of fish yields from a river to be the total area of its drainage basin.

Rivers may also have relatively high yields because even large rivers are easier for fishermen to exploit fully than are large lakes. Furthermore, many of the fish that are caught in rivers have moved into them from lakes or the sea, so their growth has occurred primarily in ecosystems outside the river.

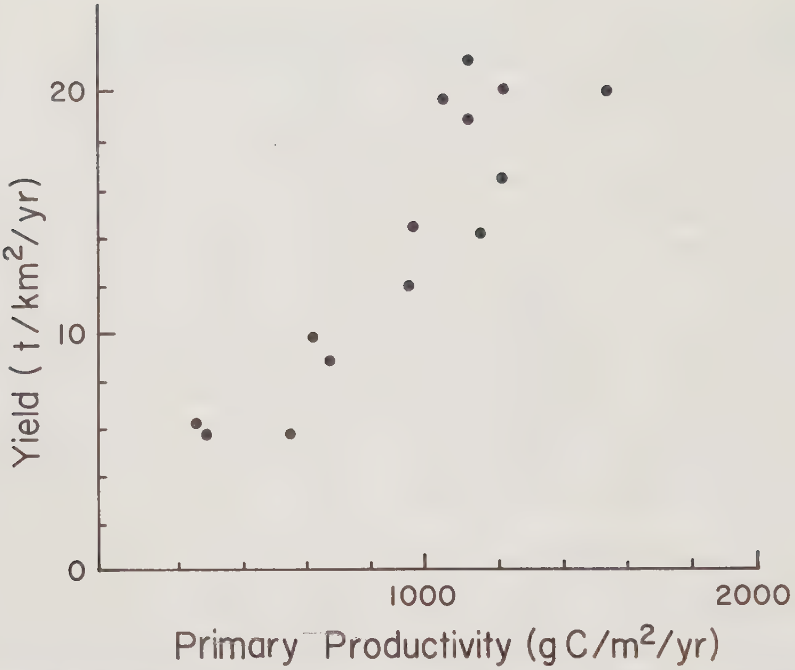

Fig. 4. Fish yields and primary productivity in tilapia ponds, based upon Almazan and Boyd (1978) (r = .89).

Table 4. Fish yields from tropical rivers.

River	Location	Catch[a]	Source
Ganges	Bangladesh	78	FAO (1976)
Niger	Benin[b]	44	Welcomme (1972b)
Lower Mekong	Viet Nam	41	R. Welcomme, pers. comm.
Mahaweli	Sri Lanka	34	Indrasena (1970)
Lubuk Lampan	Indonesia	24	Arfin and Arfin (1976)
Shire	Mozambique	13	R. Welcomme, pers. comm.
Kamulondo	Zaire	11	Poll and Renson (1948)
Oueme	Benin[b]	10	CTFT (1957)
Oueme	Benin[b]	6.5	Welcomme (1972b)
Niger	Niger	5.2	Dobrovici (1971)
Central Delta	Niger	4.5	Konare (1977)
Senegal	Senegal	4.3	Reizer (1974)
Pendjari	Benin[b]	3.5	Welcomme (1972b)
Magdalena	Colombia	3.3	Bazigos et al. (1977)
Benue	Nigeria	3.1	Mothwani (1970)
Niger	Nigeria	3.0	Mothwani (1970)
Kafue	Zambia	2.0	Zambia (1965)
Rufiji	Tanzania	1.9	R. Welcomme, pers. comm.
Kafue	Zambia	1.6	Zambia (1971)
Cross	Nigeria	1.0	R. Welcomme, pers. comm.
Barotse	Zambia	0.7	Zambia (1974)
Okawango	Namibia[c]	0.5	R. Welcomme, pers. comm.
Upper Amazon	Brazil	.02	FAO (1979)

[a] In t/km of river reach.

[b] Formerly Dahomey.

[c] Formerly S.W. Africa.

ESTUARIES AND LAGOONS

Estuaries and coastal lagoons have a mixture of freshwater and saltwater that may vary considerably in salinity at different times of the year. An estuary is subject to tidal mixing whereas a lagoon is not. Estuaries can have considerable impact on the adjacent marine fisheries because they serve as nursery areas for many fish that move out to sea at a later stage in life. Estuaries and lagoons are usually shallow, only a few meters in depth, and secondary production is often concentrated in the sediment (with its short benthic food chains) rather than in the water column. The sediment has an important role, even though it often does not itself contribute the major portion of the primary production (particularly when the water is turbid).

Saila (1975) has reviewed the ecology of estuarine fish production and Hickling (1970) has reviewed estuarine fish culture. Table 5 lists the fish yields of some tropical coastal lagoons and estuaries. The yields from both estuaries and lagoons are generally higher than the yields from lakes and rivers. This is due partly to the shallowness of estuaries and lagoons and partly to the nutrients they receive from rivers. It may also be due to the large quantity of plant materials they receive from their shoreline. This is particularly so for estuaries that are bordered by mangroves. The highest fish yields in estuaries and lagoons occur where intensive aquaculture is practiced.

CONTINENTAL SHELF

Table 6 shows the demersal and pelagic MSYs of the fisheries of continental shelves on a broad geographic scale. In general, the pelagic and demersal components make similar contributions. The highest MSYs occur with anchovies and herring, which are species with short food chains, in upwelling areas which show the highest levels of primary production recorded in oceanic waters.

Table 7 shows the estimated MSYs of some demersal multispecies fisheries in tropical coastal areas, and Fig. 6 illustrates the information behind some of the catch-effort MSY estimates in Table 7. A regression analysis of MSY against primary productivity and depth showed a significant relation only with depth (Fig. 7), the higher MSYs appearing at depths less than 50 m. There was a weak positive correlation between primary productivity and fish yields ($r = 0.24$), but primary productivity explained none of the variation in yields beyond what was explained by depth. It is worth noting that Qasim (1979) found the average primary production of Indian coastal waters shallower than 50 m to be about six times that in waters deeper than 50 m. The MSYs above and below 50 m in Table 7 differ in about the same proportion.

Table 8 presents estimated MSYs for some tropical continental shelf pelagic fisheries. These MSYs have a significant relationship with primary productivity (Fig. 8), but not with mean depth. It is interesting to note that this is the opposite of demersal fisheries, where mean depth rather than primary production best predicted yields. An explanation for the stronger correlation between pelagic yields and primary productivity may be the direct connection of pelagic fish to the planktonic food chain (Petersen and Curtis 1980), whereas demersal fish may have much less direct connection to

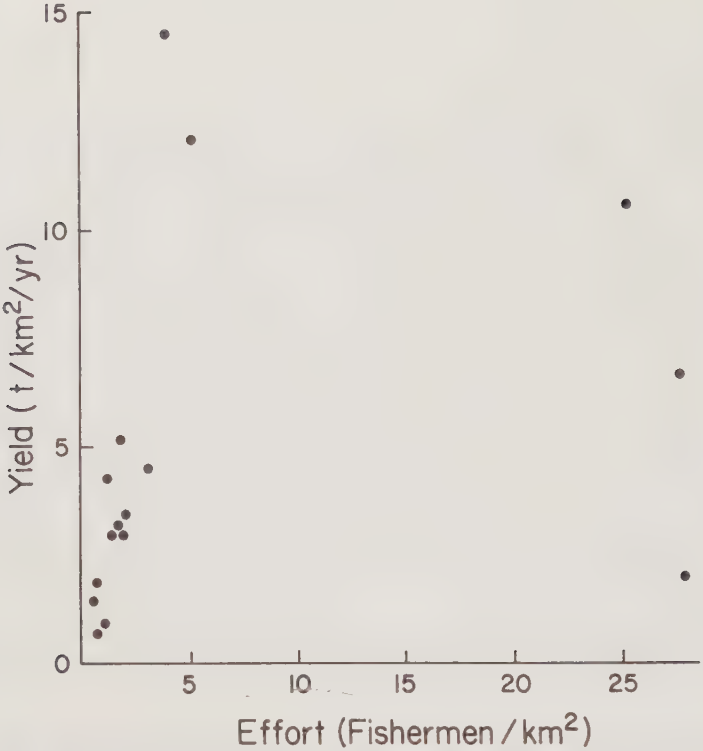

Fig. 5. Fish yields and fishing effort on tropical rivers (from Welcomme 1976).

Table 5. Fish yields from tropical estuaries and coastal lagoons.

Name of water body	Country	Area (km^2)	Catch (t/ km^2/yr)	Source
—	Taiwan (China)*		94-250	Lin (1968)
Aheme	Benin*, **	85	86	Welcomme (1972b)
—	India*		86-124	Pakrasi et al. (1964)
Nakove/Pio Novo	Benin*, **	157	56	CTFT (1969)
—	Philippines*		50-100	Frey (1947)
—	Philippines*		50	Tang (1967)
—	Philippines*		47	Rabanal (1961)
Ovidah, Grand Popo, Awo channel	Benin*, **	14	28	Welcomme (1972b)
—	Singapore*		25	Le Mare (1949)
—	Hawaii*		20	Cobb (1901)
Ebrié	Ivory Coast	556	16	Durand et al. (1978)
Sakumo	Ghana	1	15	Pauly (1976)
—	Java*		14-63	Schuster (1952)
Unare	Venezuela	54	14	Okuda (1965)
—	Morocco		13	Belloc (1938)
Cienaga Grande	Colombia	450	12	INDERENA (1974)
—	India		11-17	Pillay (1954)
Tacarigua	Venezuela	63	11	Gamboa et al. (1971)
Piritu	Venezuela	22	5.8	Carvajal (1972)
Mandapam	India	4	5.6	Tampi (1959)
Tamiahua	Mexico	659	4.7	Garcia (1975)
Chillca	India	1,036	3.7	Jhingran and Natarajan (1969)
Pangalanes	Madagascar	98	3.7	Lasserre (1979)
Anony	Madagascar	23	2.8	Moulherat and Vincke (1968)
Pulicat	India	392	2.6	Jhingran and Gopalakrishnan (1973)
Maracaibo	Venezuela	14,344	1.9	Nemoto (1971)
Jiquilisco	El Salvador	121	1.7	Hernandez and Calderon (1974)

*Includes aquaculture (without fertilization or feeding).

**Formerly Dahomey.

the primary production in the water column above. The lack of correlation between pelagic yields and depth may also be because coastal pelagic fishes probably range over a larger geographic area than demersal fish, so the depth in the area they are fished may not accurately represent the mean depth of their entire habitat.

Yesaki (unpub. data) observed a positive association between total multispecies fish yields and primary productivity when comparing a number of tropical and temperate continental shelf fisheries. He also observed a negative association between total yields and the number of species in the fishery.

Coral Reefs

The coral reef is an ecosystem in which the reef surface provides a substrate for growth of algae, both free-living and symbiotic with coral polyps. This fosters the maximum biological production possible within the limits of nutrients available in the surrounding water.

Table 6. Estimated maximum sustainable yields (t/km^2/year) for tropical continental shelf areas (from Gulland 1971 except where noted otherwise).

Region	Minimum Pelagic	Minimum Demersal	Minimum Total	Maximum Pelagic	Maximum Demersal	Maximum Total
NE Atlantic	0.8	0.6	1.4	7.3	8.0	15.3
NW Atlantic	1.8	1.8	3.6	7.0	7.0	14.0
NW Pacific	0.6	1.7	2.3	8.5	4.0	12.5
Indian Ocean[a]	0.7	1.4	2.1	4.3	5.5	9.8
E Central Atlantic	4.0	1.2	5.2	5.0	2.5	7.5
South China Sea[b]	0.2	0.8	1.0	2.4	4.3	6.7
W Central Atlantic	0.7	0.2	0.9	3.2	2.5	5.7
		Upwelling				
SW Atlantic	1.5	6.0	7.5	17.5	10.0	27.5
Peru[c]	—	—	—	1.0	21.9	22.9

[a] Yesaki (unpub. data).
[b] Menasveta et al. (1973).
[c] Murphy (1972).

Table 9 lists the fish yields of some coral reefs. The range is similar to that for other continental shelf fisheries, despite the higher primary productivity of coral reefs. Marshall (1980) reviewed potential fish yields from coral reefs and found a range of 0.8 to 5 t/km^2/year (see Fig. 9). He noted the observation of 14-20 t/km^2/year* for an intensively exploited reef in the Philippines (Alcala 1981) but questioned the generality of that observation. However, recent work by Wass (in press) on an intensively exploited reef in Samoa has estimated the finfish yield to be 18 t/km^2/year, suggesting that some of the lower estimates from previous studies may not reflect the yields of fully exploited reef systems. Fig. 10 shows the relation between the number of fishermen and the yield which has been realized on some coral reef fisheries.

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*Editorial note: Marshall (1980) cites Alcala as having suggested a figure of 15 tonnes/km^2/year; it is the actual figures given by Alcala (1981) which are given here.

Table 7. Estimated maximum sustainable yield of tropical demersal marine fisheries.

Location	MSY ($t/km^2/yr$)	Depth (m)	Area (km^2)	Primary productivity ($gC/m^2/yr$)[a]	Estimation method	Source
North Coast Gulf of Mexico	6.7	0-110	111,210	135	Research Survey (0.5 B_o)	Klima (1977)
U.S. Atlantic Coast (N. Carolina—Florida)	5.5	0-110	125,000	135	Research Survey (0.5 B_o)	Klima (1977)
Gulf of Thailand	3.9	0-50	179,000	365	Catch vs. Effort (Fig. 6a)	SCS (1978)
Philippines	2.8	0-200	152,700	135	Research Survey (0.5 B_o)	Aoyama (1973)
North Coast of Java	2.6	0-50	26,160	180	Catch vs. Effort (Fig. 6b)	SCS (1979)
Sunda Shelf—South	2.3	0-50	267,900	75	Research Survey (0.482 B_o)	SCS (1978)
South China Sea	2.0	0-200	500,000	45	Research Survey (0.5 B_o)	Aoyama (1973)
West Coast of Florida	1.8	0-110	179,280	135	Research Survey (0.5 B_o)	Klima (1977)
Sunda Shelf—NW Borneo	1.7	0-50	62,900	75	Research Survey (0.482 B_o)	SCS (1978)
South Coast of Kalimantan (Borneo)	1.5	0-50	113,590	135	Research Survey (0.5 B_o)	SCS (1979)
Sunda Shelf—NW Borneo	1.1	50-200	69,700	75	Research Survey (0.482 B_o)	SCS (1978)
Gulf of Thailand	1.1	50-200	126,700	365	Research Survey (0.482 B_o)	SCS (1978)
Sunda Shelf	0.8	50-200	398,500	135	Research Survey (0.482 B_o)	SCS (1978)
U.S. Atlantic Coast (N. Carolina—Florida)	0.5	110-548	20,480	45	Research Survey (0.5 B_o)	Klima (1977)
North Gulf of Mexico	0.5	110-548	44,070	45	Research Survey (0.5 B_o)	Klima (1977)
West Coast of Florida	0.4	110-548	72,120	45	Research Survey (0.5 B_o)	Klima (1977)

[a] Primary productivity estimated from a world map in FAO (1972).

As a reef fishery is generally a patchwork of coral reef (which is highly productive) and sandy bottom (which is not so productive); the yield per unit area that is calculated for a reef can depend very much upon the size of the area and the percentage of that area which is actually covered by coral or other hard substrate. Some fisheries records cover a large area of many square kilometers, only part of which is actually covered by coral, whereas other records of fish yields apply to very small areas that are entirely coral reef. The productivity of a reef may also vary with the complexity of its vertical structure.

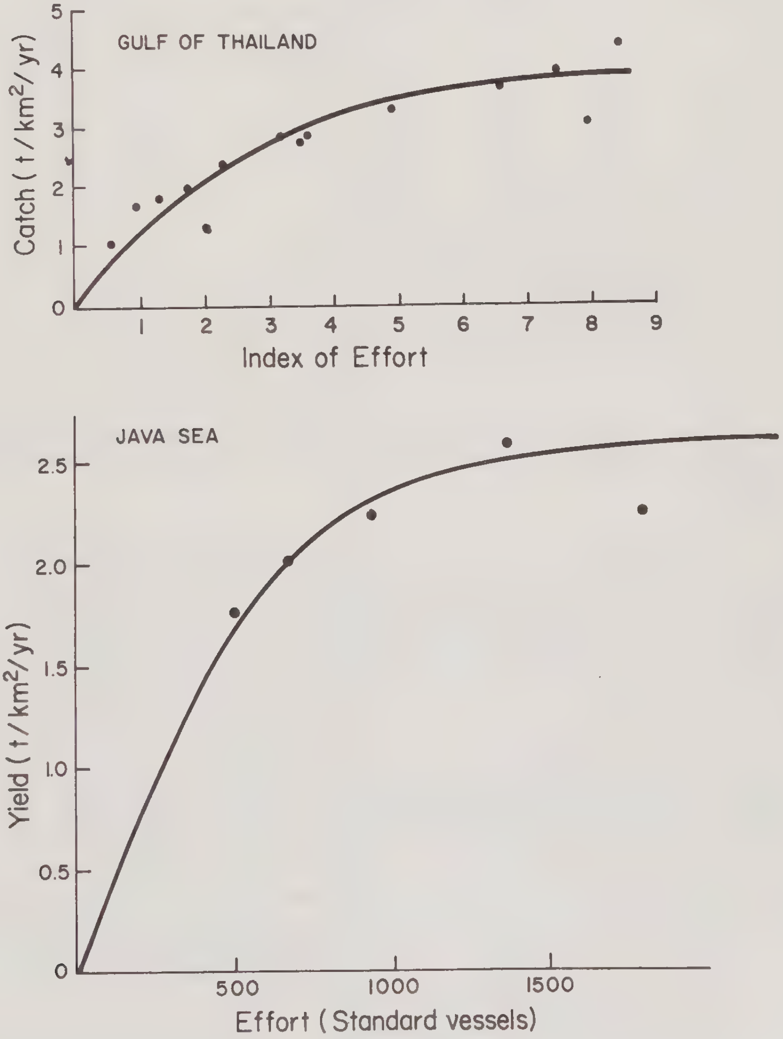

Fig. 6. Estimation of maximum sustainable yield for continental shelf demersal fisheries (from SCS 1978 and SCS 1979). The points in the graph represent different years in the history of the fishery.

Table 8. Estimated maximum sustainable yields of tropical pelagic fisheries.

Location	MSY ($mt/km^2/yr$)	Depth (m)	Primary productivity ($gC/m^2/yr$)	Estimation method	Source
Java Sea (N. Coast of Java)	6.02	0-50	180	0.5 B_o	SCS (1979)
South Atlantic	4.43	0-550	135	Research Survey (0.5 B_o) and Landings	Klima (1977)
Sumatra (West Coast)	4.28	0-40	130	Research Survey (0.5 B_o)	SCS (1979)
India (West Coast)	3.58	0-50	180	1978 Landing	Anon. (1979)
Malaysia (West Coast)	3.38	0-100	130	Landing 1973-1974	Yesaki (unpub. data)
Gulf of Mexico (coast)	3.20	0-550	90	Research Survey (0.5 B_o) and Landings	Klima (1977)
Atlantic (South America)	2.35	0-550	135	Research Survey (0.5 B_o) and Landings	Klima (1977)
India (East Coast)	1.98	0-50	180	1978 Landing	Anon. (1979)
India (West Coast)	1.03	0-200	135	1978 Landing	Anon. (1979)
Thailand (West Coast)	1.02	0-100	55	Research Survey (0.5 B_o)	SCS (1976b)
South China Sea	0.81	0-500	45	Research Survey (0.5 B_o) and Landings	SCS (1973)
India (East Coast)	0.70	0-200	90	1978 Landing	Anon. (1979)
Philippines (offshore)	0.55	200 and more	110	Research Survey (0.5 B_o) and Landings	Menasveta et al. (1973)

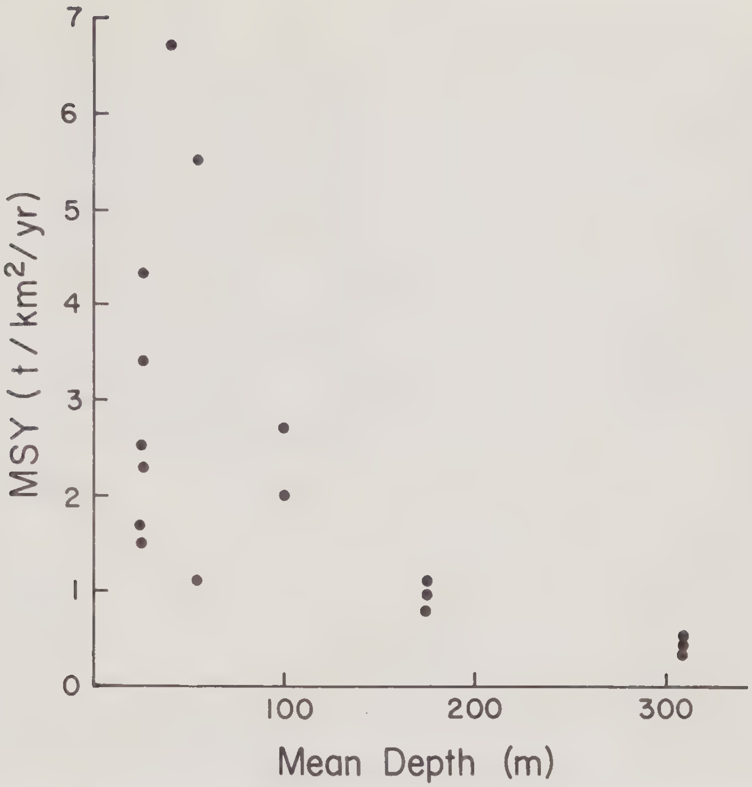

Fig. 7. Maximum sustainable yields and depth of continental shelf demersal fisheries, based on Table 7 (r = .86).

Open Ocean

Annual catches of tunas and billfishes by Japanese vessels in the western tropical Pacific, aggregated by 10-degree squares (data on file at the National Marine Fisheries Service, Southwest Center, Honolulu Laboratory) show a range of yields from 0.0025 to 0.04 t/km^2/year, with an average yield of 0.016 t/km^2/year. (This is an underestimate of the total catch because Korean vessels also fish this region but are not included in the statistics.) Catches of tunas and billfishes in the eastern tropical Pacific (Calkins 1975) suggest a range of yields from 0.002 to 0.04 t/km^2/year, with an average of 0.024 t/km^2/year. Finally, catches of tunas and billfishes in the 10-degree squares in the tropical Atlantic off the coast of Africa (ICCAT 1980) are as high as 0.05 t/km^2/year. The range of existing yields in the open ocean does not extend much below the range of MSYs for that ecosystem because much of the open ocean, like much of the continental shelves, is fished intensively by sophisticated fishing fleets.

Discussion

Relationship between Yields and Ecosystem Types

Fig. 11 summarizes the ranges of primary productivities and fish yields encountered in various tropical ecosystems. The range of fish yields is

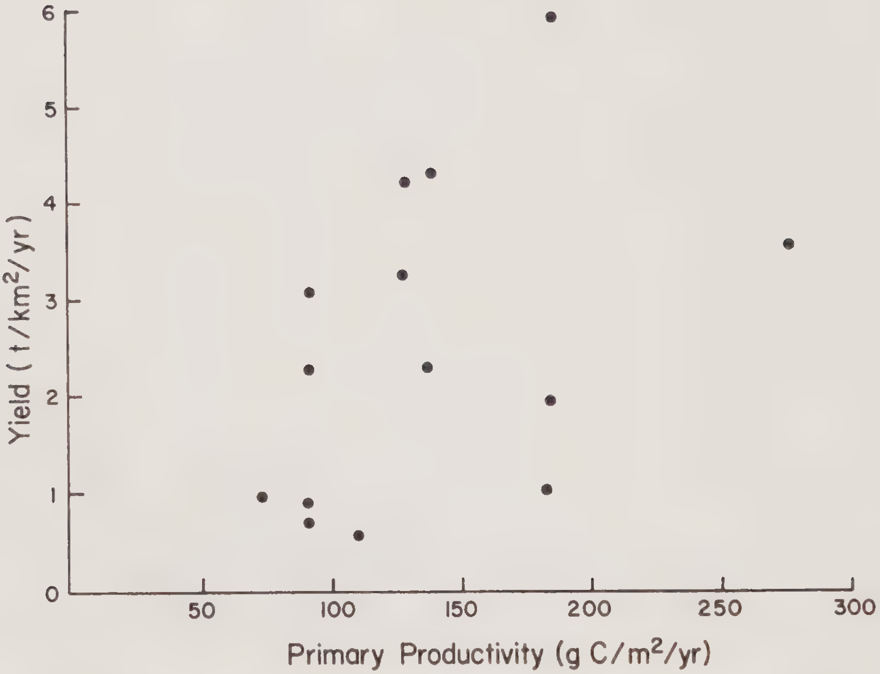

Fig. 8. Maximum sustainable yield and primary productivity of continental shelf pelagic fisheries, based on Table 8 (r = .61).

Table 9. Yields from coral reef fisheries.

Location	Area (km^2)	Catch, ((t/km^2)	Source
Samoa*	3	18^b	Wass (in press)
Philippines	1	18^b	Alcala (1981)
Samoa		8^b	Hill (1978)
Ifaluk* (Pacific)	6	5.1	Stevenson and Marshall (1974)
East Africa		5^c	Gulland (1979)
Mauritius*	350	4.7^a	Wheeler and Ommanney (1953)
Fiji		4.4^a	Bayliss-Smith (pers. comm.)
Jamaica*	2,860	4.1^c	Munro (1978)
Bahamas		2.4^a	Gulland (1971)
Puerto Rico*	2,300	0.8^b	Juhl and Suarez-Caabro (1972)
Kapingamaringi* (Pacific)	400	0.7^b	Stevenson and Marshall (1974)
Cuba*	55,000	0.5	Buesa Mas (1964)
Lamotrek* (Pacific)	44	0.45^b	Stevenson and Marshall (1974)
Bermuda*	1,035	0.4	Bardach and Menzel (1957)
Raroia* (Pacific)	400	0.09	Stevenson and Marshall (1974)

*Catch and fishing effort appear in Fig. 10.
[a] MSY based on catch-effort relation over series of years.
[b] Probably near the MSY because of heavy fishing intensity.
[c] See Fig. 9.

different in each of the ecosystems, but the ranges are so broad that most of the ecosystems overlap considerably. As a consequence, ecosystem type alone is not a precise predictor of the potential yield of a particular fishery, at least at the coarse level of ecosystem classification employed here.

There is a positive association in Fig. 11 between the primary productivities of ecosystems and their fish yields, but the relation is not very tight. Some ecosystems with similar primary productivities have very different fish yields, and other ecosystems with similar fish yields have very different primary productivities. Furthermore, the overall range of fish yields through all ecosystems is much greater than the overall range of primary productivity, indicating that fish yield is not simply responding in proportion to primary productivity regardless of the ecosystem. Primary productivity is not useful to predict fish yields unless the ecosystem is specified.

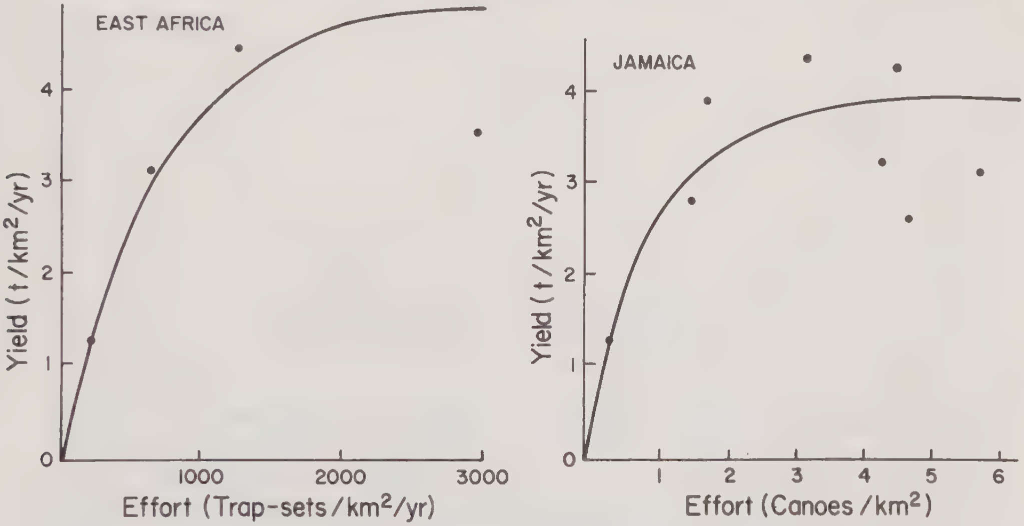

Fig. 9. Estimation of maximum sustainable yields for coral reefs [from Munro 1978 (Jamaica) and Gulland 1979 (East Africa)]. The points in the graphs represent different reef fishing locations in the same geographic area.

Table 10 shows the estimated range of efficiencies with which primary productivity is turned into fish yields in each of the ecosystems. (The real range in efficiencies for each ecosystem is probably more narrow because measurement errors would tend to broaden the range.) Lakes and reservoirs are quite similar. Rivers can have a higher efficiency, but it may be an artifact due to external inputs. The limited information on lagoons and estuaries indicates that the lower end of their range falls within the same range of efficiencies as lakes. The upper end is higher because of intensive aquaculture. Continental shelf fisheries appear to have a slightly higher efficiency than lakes, while upwelling areas have much higher efficiencies due to short food chains. The efficiency of coral reefs, which typically have a multitude of species, can be somewhat lower than the rest of the continental shelf. The efficiency of open oceans is less by an order of magnitude, presumably because of longer food chains.

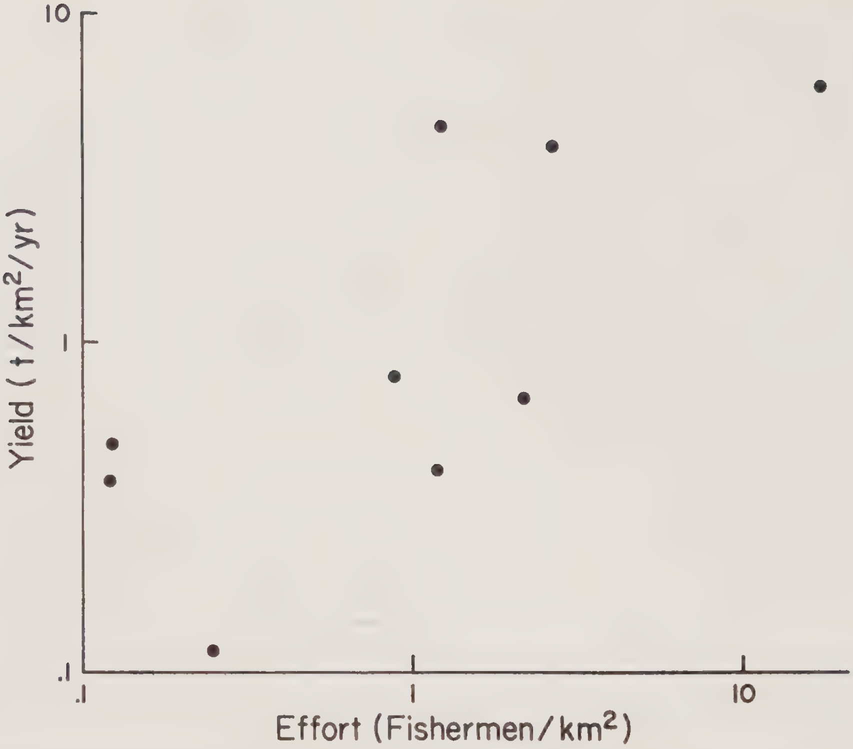

Fig. 10. Fish yields vs. fishing effort in coral reefs (based upon reef data in Table 9).

One reason the ecosystems appear to differ in their efficiencies is because some of them can exploit primary production that is elaborated outside the ecosystem, whereas others do not have an input of such materials. If the total productivity base of each ecosystem—including both primary production and organic matter from outside—were used in place of primary production alone, the relation between the productivity base and potential fish yield might be more universal regardless of the ecosystem. However, even with a better measure of the productivity base, different ecosystems could still differ in the food-chain structure which determines the efficiency of translating the resource base into fish yields.

Ecosystem and primary productivity can together predict potential fish yields better than either one alone. Nonetheless, there is considerable variation in yields that remains unexplained even when both are taken into account (Figs. 3 and 10), though it is possible the predictions could be more precise if the ecosystem classification were more refined. Even though such predictions can be helpful for rough inventories of potential fish yields, it is unlikely they will ever be precise enough for managing particular fisheries in the absence of other information about yields.

YIELD ASSESSMENT AND MANAGEMENT

The potential fish yield from an ecosystem cannot be inferred from catch records without reference to the fishing effort behind those records. The relationship between catch and effort is customarily displayed by means of graphs where different levels of effort are found at different locations within the same fishery (e.g., Fig. 9) or where different levels of effort have occurred at different times in the history of the fishery (e.g., Fig. 6). It is possible from catch-effort graphs to see if the fishing effort has been intense enough for the potential yield of the fishery to be expressed in actual yields. However, the yield from a multispecies fishery is not only a matter of how much fishing, but also what kind of fishing. Potential yields from different ecosystems can only be assessed in this context.

Table 10. Ratio of fish yields to primary productivity.[a]

Ecosystem	Range	Geometric mean
Coastal upwelling	.005 - .013	0.0081
Rivers	.005 - .01	0.0071
Ponds	.001 - .01	0.0032
Lagoons and estuaries	.0008 - .01	0.0028
Continental shelf	.0003 - .003	0.00095
Lakes	.0004 - .0016	0.00080
Reservoirs	.0002 - .002	0.00063
Coral reefs	.0002 - .0008	0.00040
Open ocean	.00001 - .0002	0.000045

[a] The ratios in this table are based on primary productivity estimates in Bunt (1975), Beadle (1974), Conner and Adey (1977), Cushing (1969), Edwards (1978), Gerlotto et al. (1976), Hempel (1973), Kaliyamurthy (1973), Kinsey (1979), Koblentz-Mishke et al. (1970), Likens (1975), Plante-Cuny (1977), and Rodriguez (1963). The ratios were calculated as the carbon yield of fish (assumed to be one-tenth of wet weight) divided by primary productivity (in carbon units).

There are two principal ways that the total harvest from a multispecies fishery can be increased by manipulating the kind of fishing:

- — more intricate harvesting;
- — restructuring the food web.

We have already observed that the highest yields from coral reefs occur where there is intense, intricate fishing. Higher yields can also be achieved by altering food web structure by:

- — shortening the food chain between primary production and fish production;
- — reducing fish consumption by predators which compete with fishermen.

Examples are the introduction of herbivorous or sediment-feeding fish to a fishery or the implementation of special measures to reduce predation (e.g., cage culture or intense fishing of predators).

The fishery of Lake Victoria (East Africa) illustrates these points. Lake Victoria has a multispecies fishery (12 commercial genera and more than a hundred species) which, like many other inland fisheries, shows signs of overfishing: declining fish sizes and disappearance of major commercial species. The diversity of fishing intensities and fishing gear around the shoreline of Lake Victoria has led to a similar diversity of yields and species composition in the catch. The result is a series of unplanned "experiments", which Marten (1979a, 1979b) has analyzed statistically to summarize the impact upon the stocks of the amount of fishing and the kind of fishing. The main interpretive tool was a curvilinear regression of catch versus effort,

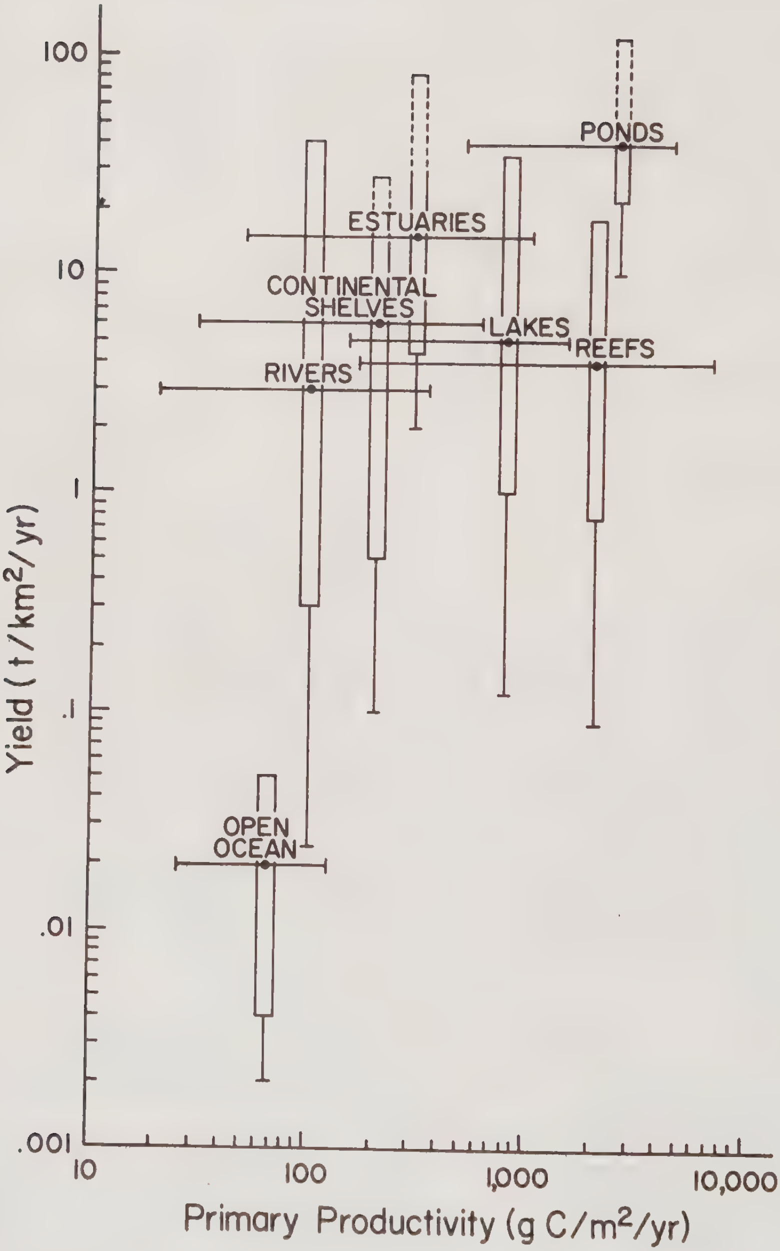

Fig. 11. Ranges of fish yields and primary productivities in various tropical ecosystems. Dots at the intersection of ranges represent modal values. Thickened portions of the bars represent the range of maximum sustainable yields. Dashed projections at the top of the ranges for estuaries and ponds represent elevated yields from aquaculture with fertilization (but not supplemental feeding). The dashed projection for continental shelves represents higher yields which occur in areas of upwelling. Primary productivity estimates are based on the references listed in Table 10.

in which the total catch (summed over all species) occupied one dimension and effort occupied six dimensions corresponding to six categories of fishing gear.

Above a certain fishing effort, the total multispecies catch in Lake Victoria is not affected much by fishing effort *per se*, but it is very much affected by the kind of fishing gear employed. There is no mix of gear which is optimal for all species in the fishery. What is optimal for one species may underexploit or destructively exploit another species. Fishing gear also has indirect ecological effects upon fish species that may not even be captured by that kind of gear, because of predation and competition, and these effects may lead to successional changes in the species composition of the fishery.

The optimal mix of gear for the fishery as a whole is a compromise. In the case of Lake Victoria, the optimal mix emphasizes intensively harvesting species at the end of short food chains (which are part of Lake Victoria's native fish fauna) and fishing down large fish that prey upon these species. There is no indication that even the heaviest fishing leads to lower yields if the optimal mix is employed. This suggests the practical conclusion that maximizing the yield from a multispecies fishery may be as much a matter of developing the infrastructure to encourage the right kind of intensive fishing as of restricting fishing practices which appear harmful.

Most of the management attention in fisheries to date has been devoted to yields, but the management of multispecies fisheries may be equally a matter of insuring a desirable species composition in the fishery. Although heavy fishing may not in itself significantly reduce the total yield from a multispecies fishery, it is quite common for heavy fishing (or the wrong kind of fishing) to change the composition, and therefore economic value, of the fishery. A change in species composition can also influence total yields to some extent because of food chain and predation effects.

A Habitat Perspective

A finer view of aquatic ecosystems than has been customary for fisheries purposes will be necessary for more effective management and yield assessment of multispecies fisheries. Substrate type is one way of distinguishing different habitats within the broader ecosystem, and Wanjala (1978) has shown that different sections of the Lake Victoria shoreline with different substrates (e.g., stony or muddy) are inhabited by different fish communities. The same is true in Hawaii, where different demersal fish communities are found at different depths offshore (Ralston and Polovina, in press); and different inshore substrates, such as lava and sand, each have their characteristic fish communities, potential yields and management needs, even though all are part of the broader shore ecosystem (Hawaii Coastal Zone Fisheries Management Program 1980). Each of these habitats has its own characteristic fisheries succession in response to fishing and each requires specific management decisions.

A habitat approach emphasizes attention to species composition (including a classification of fish communities), how different fish communities are associated with different habitats, and how community composition responds to human activities (including fishing practices) that impinge upon the fishery (Smith et al. 1973; Marten 1981). This perspective does not mean that massive amounts of quantitative data are required in much more detail than before. The data need only be roughly quantitative, but they must be sensitive to species composition. (This approach to species management is analogous in many respects to range management, where attention is given to forage species composition and how this changes under grazing pressure.) Habitats can be mapped (Aecos 1979), and because fishermen are generally precise about where they fish, it is possible at least in theory to maintain catch records on a habitat basis.

A habitat perspective in multispecies fisheries management and assessment may mean that the maintenance of habitat quality will be as important as the regulation of fishing effort. Although the production of a multispecies fishery can be manipulated to some extent by adjusting the harvesting regime, the yield from that fishery can be reduced immensely by habitat destruction. This includes destructive fishing practices such as the use of dynamite, poisons, and seines and trawls that scrape across the bottom and disrupt the production of fish food or spawning of fish. Equally important, however, are non-fishing activities that may cause even more serious destruction of fishery habitat, such as the siltation of coral reefs due to runoff from mining activities or pollution due to sewage, industrial effluents or oil spills. Pollution problems will increase as industrialization increases in the tropics, particularly under impetus from some countries to transfer their most polluting industries to developing countries.

This kind of fisheries management and assessment is complicated. It is not realistic to depend upon ecological theories to predict what will happen in every specific situation. Multispecies fisheries management and yield assessment will have to remain empirical, based on observations of how fish community composition and yields change under different circumstances, taking advantage of "experiments" provided by existing fishing activities in different places with different fishing conditions and different histories. It will have to be pragmatic and adaptive in the sense described by Holling (1978) for adaptive environmental management, relying upon monitoring to anticipate unwanted "surprises", and developing new approaches for keeping options open in dealing with such surprises.

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Discussion of the Paper by Drs. Marten and Polovina

Dr. Gulland suggested that a graph of total catch/km^2/year versus the number of fishermen/km^2, as in Fig. 1, may be of more use than the authors assumed. If a fishery approaches its maximum yield at the same density of fishermen, regardless of how large or small the MSY may be, then the cluster of level points in Fig. 1 would suggest that yields approximate the MSY whenever there are two or more fishermen/km^2. This question deserves further study. However, Dr. Marten was still of the opinion that lakes with a very low level of production could reach their maximum yield at a significantly lower number of fishermen.

Dr. Gulland asked what area was being used for river fisheries, and Dr. Marten replied that it was the area covered by the river at flood level. Dr. Gulland felt that it could make a big difference if the flood plain is included because it can add considerable production to the river.

Dr. Larkin commented that the level of exploitation of a lake depends very much on its location in relationship with the people who exploit it, citing the lakes in the north of Canada which are virtually unexploited because there are so few people around them. Dr. Sainsbury added that it is also a matter of what people are willing to do with the fishery. He wondered what yields would be like in the open ocean if people were prepared to eat myctophids or in coral reefs if they would eat pomacentrids. He has MSY estimates for the Australian northwest shelf that range from 4,000 t/year for an Australian-style fishery based on harvesting only large fish, to 30,000 t, if one is prepared to fish everything that is there.

Mr. Jones was impressed with the high productivity of shallow lakes and noted the importance of shallow, inshore areas as fish nursery areas. The total productivity of areas like the North Sea may be higher than is recognized because the higher inshore productivity is usually not taken into account. Dr. Murphy questioned the general importance of inshore areas as nurseries, citing the northwest shelf of Australia as an example where there is no evidence that inshore areas are nurseries. Dr. Marten commented that the inshore areas of Lake Victoria are nurseries for tilapia and that abuse of those inshore areas with seines appears to have contributed to the decline of tilapia. Dr. Pauly noted that graphs of fish size against depth invariably show the larger fish to be at greater depths. Dr. Gulland noted that it is difficult to know how much of the fish production has actually occurred inshore or offshore because many fish migrate from one area to the other.

Mr. Simpson pointed out that coral reefs that are directly offshore may have different yields from the barrier reef type. He also remarked that the high bird populations in many coastal lagoons may be taking a substantial portion of the fish production.

Dr. Sale suggested that, in addition to different food chains being responsible for the wide range of yields in the same ecosystem, different taxonomic groups and associated differences in the physiology of the fish may also be important. Some kinds of fish may be more efficient at converting their food to usable fish flesh than others. Mr. Jones cited the ability of *Sarotherodon niloticus* and one of the zooplankters in Lake George to digest the abundant blue-green algae that are indigestible for most animals. Dr. Marten speculated that the variation in digestibility of the organisms along the food chain could also influence the overall efficiency of transforming primary production to fish yields.

Following the observations on Lake Victoria that decline in total catch at high fishing efforts were a consequence of destructive fishing practices rather than an increase in fishing effort *per se*, there was a discussion of whether the total catch versus effort curve drops or remains high with increasing effort.

Dr. Pauly noted that the stocks of small fish species in the Gulf of Thailand have collapsed under fishing pressure, apparently due to the additional burden of heavy predation from larger fish, as has been the case with small fish like *Haplochromis* in Lake Victoria. However, Dr. Murphy felt that trawling the Gulf of Thailand should put as much fishing pressure on the small species as the large species and that a manipulation of gear-specific effort is only applicable to artisanal fisheries. Dr. Sainsbury expressed the need for better catch statistics because it is difficult to know with the present information just how hard the small species in the Gulf of Thailand have been fished.

Discount Factors and Risk Aversion in Managing Random Fish Populations

ROY MENDELSSOHN[1]

Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, USA

MENDELSSOHN, R. 1982. Discount factors and risk aversion in managing random fish populations. Can. J. Fish. Aquat. Sci. 39: 1252–1257.

The effects of changes in the discount factor as compared with the effects of changes in risk aversion are examined for a simple stochastic model of fish population dynamics. Numerical results suggest that both optimal harvesting strategies and the resulting population dynamics are insensitive to changes in the discount factor, whereas changes in the degree of risk aversion in the utility function do cause significant changes in both. When risk averse utility functions are viewed as total revenue curves with marginal prices that decrease with supply, the results suggest that the more sensitive price is to supply, then the resulting optimal harvesting policy is smoother. Theoretical results are presented which suggest these results are robust beyond the specific model.

Key words: discount factors, risk aversion, population dynamics, randomness

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Nous analysons, sur un modèle stochastique simple de dynamique des populations, les effets de changements du facteur escompte comparativement aux effets de changements du facteur aversion contre le risque. Les résultats donnent à penser que les stratégies de récolte optimale, ainsi que la dynamique des populations qui en résulte, ne sont pas influencées par les changements du facteur escompte. Par contre, le degré d'aversion contre le risque dans la fonction utilité entraîne en fait des changements significatifs dans les deux. Quand on considère les fonctions utilité opposées au risque en termes de courbes de revenus totaux, avec prix marginaux qui diminuent en même temps que l'offre, les résultats suggèrent que plus le prix est sensible à l'offre et plus douce est la politique de récolte optimale qui en découle. Nous présentons des résultats théoriques vraisemblablement applicables au-delà de ce modèle particulier.

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THE standard literature (see Clark 1976, 1980; Anderson 1977; and references therein) on dynamic, deterministic fishery optimization models has stressed the importance of the discount factor ($1/(1 + i)$, where i is the interest rate) in determining optimal harvesting strategies. The discount factor has been emphasized because an optimal harvesting strategy depends continuously on the discount factor, and a stock will be optimally harvested to extinction if the rate of growth of the population is less than the rate of discount (Reed 1974; Clark 1976). Related results have been established for stochastic harvesting models (Reed 1974; Mendelssohn 1980b; Mendelssohn and Sobel 1980), though in a stochastic model the population dynamics may drive the population to extinction even though the harvest levels have not left the remaining population at or near zero.

The presumed sensitivity of an optimal harvesting strategy to changes in the discount factor is important, as a standard procedure for representing increased risk to a manager of a fishery in face of uncertainty is to decrease the discount factor. Even at first glance this is a naive approach, as it assumes a constant attitude towards risk regardless of the initial population size or harvest decision.

What would appear to be a more sophisticated approach towards risk is to assess the manager's utility function and use this as the objective function. This approach to managing fisheries and other natural resources is given in Hilborn and Walters (1977), Keeney (1977), and Holling (1978); a general discussion can be found in Keeney and Raiffa (1976).

One way to compare these differing approaches is to see how changes in the discount factor and changes in the degree of risk aversion affect the policy that should be followed. In this paper this is done for one empirical stochastic model of a fishery. In particular, the actual sensitivity of an optimal harvesting strategy to changes in the discount factor is compared with its sensitivity to changes in the degree of risk aversion in the utility function. Further changes in the population dynamics of a stock being managed under an optimal

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[1] Present address: Pacific Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93942, USA. Work done while at Center for Coastal Marine Studies, Applied Sciences 254b, University of California at Santa Cruz, Santa Cruz, CA 95064, USA.

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harvesting policy are examined as both the discount factor and the degree of risk aversion vary. Also, the appendix presents theoretical results which suggest the numerical results presented are robust over a wide class of models.

The Model

The model to be analyzed is a stochastic version of a Ricker spawner–recruit curve put forward by Mathews (1967) for salmon runs in Bristol Bay. Let x_t be the recruits in period t, and y_t the spawners. If x is observed and a decision y is taken, a one-period utility $g(x, y)$ is received. Without loss of generality, $g(x, y)$ can be the expected value (over the random variable θ) of some other utility $h(x, y, \theta)$. Hence the model indirectly includes economic uncertainty.

The utility in period t is discounted by a factor β, $0 \leq \beta < 1$. The recruits in period $t + 1$ are a random function of the spawners in period t and a random variable d,

$$(1) \quad x_{t+1} = d4.084y_t \exp\{-0.8y_t\}; \ \ln d \sim N(0, 0.2098)$$

where $N(0, \sigma^2)$ denotes a random variable that follows a normal distribution with mean zero and variance σ^2.

The problem is to maximize the expected discounted utility.

$$(2) \quad \text{maximize} \sum_{t=1}^{\infty} \beta^{t-1} g(x_t, y_t)$$

such that $x_t \geq y_t \geq 0$; Eq. (1).

Computational techniques for solving Eq. (2) and related policy questions are discussed in Mendelssohn (1980b). A 100-point grid is used with no absorbing (zero) population size.

Two different utility functions are examined for $g(x, y)$. The first is $v_1 = 0.5 \ln (x_t - y_t)$ while the second is $v_2 = (x_t - y_t)^\lambda$, for $\lambda = 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, 0.95, 1.0$. These utility functions are plotted in Fig. 1. Utility functions are said to be absolute risk averse (Merton 1969, 1971; Keeney and Raiffa 1976) if $-u''(z)/u'(z) > 0$ for a function $u(z)$. The Pratt measure of relative risk aversion is $-u''(z)z/u'(z)$. Basically, a utility function is risk averse if a certain return is preferred to a lottery with equal or greater value in expectation.

The two utility functions v_1 and v_2 are members of the HARA (hyperbolic absolute risk averse) family of utility functions (Merton 1969, 1971). In particular, if R_1 is the measure of absolute risk aversion, and R_2 is the measure of relative risk aversion, then for v_1, $R_1 = 1/z$ and $R_2 = 1$; for v_2, $R_1 = (1 - \lambda)/z$ and $R_2 = 1 - \lambda$, where $z = x - y$ is the amount harvested. Both v_1 and v_2 have constant relative risk with respect to the amount harvested. However, it is clear that the relative risk aversion for v_2 changes linearly with λ. Hence λ is a measure of the relative degree of risk aversion. For λ approaching zero, the manager is totally risk averse, whereas for $\lambda = 1$ the manager is risk neutral. The utility function v_1 is the limiting case of v_2 as λ approaches zero.

The utility functions v_1 and v_2 are not as rich as they might be given that they only depend on (x_t, y_t) through $z_t = x_t - y_t$. However, there exists little empirical basis for choosing more complicated utility functions that can be given meaningful, practical interpretations. Both v_1 and v_2 can be viewed as total revenue curves. Taking derivatives $v_{1'} = 0.5/z$ ($v_{2'} = \lambda z^{\lambda-1}$) and $v_{1''} = -0.5/z^2$ (respectively, $(1 - \lambda)z^{\lambda-2}$). The first derivative is the marginal price for a supply of z units of fish, with the marginal price decreasing with increasing supply. Therefore, using v_1 and v_2 as the one-period utility functions can be viewed as examining the effect of dropping the usual economic assumption of perfect competition. This is treated analytically in some detail in Mendelssohn and Sobel (1980).

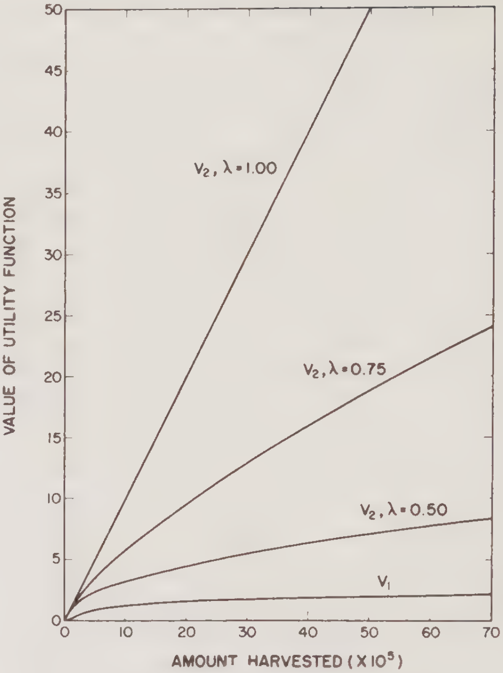

FIG. 1. Graph of the different utilities function.

It is worth emphasizing that "risk" is used here in a very specific way. In some papers, risk is used to denote the randomness in the population dynamics. Here, it is assumed that all random variation in the population is contained in the random variable d. No effort is made to discuss the actual merits or accuracy of Mathew's model. Instead the model is taken as given.

Also, sometimes risk is used to denote undesirable events that could happen to the population that are not directly reflected in the utility function. The risk of extinction or of very small population sizes is one such example. This problem is treated in Mendelssohn (1978).

Risk in this paper denotes the gamble the decision maker faces in the certain reward of the given return function (in this case harvest) this period versus the uncertain return next period. The return function is assumed given. For many problems, the choice of the appropriate return function is crucial (Mendelssohn 1980b).

Results

Optimal harvesting policies and the resulting population

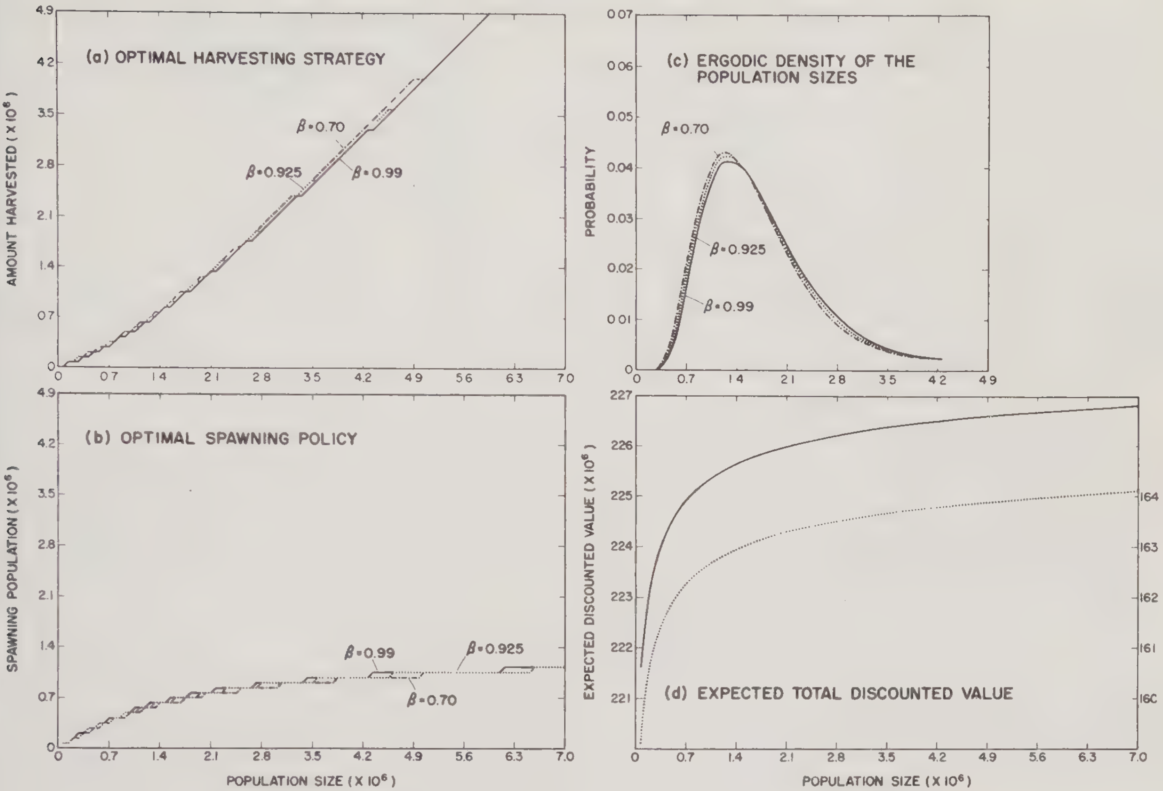

FIG. 2. Effects on an optimal policy and optimal value from varying the discount factor.

dynamics were calculated for both classes of utility functions for discount factors of 0.99, 0.95, 0.925, 0.9, 0.85, 0.80, and 0.70. These discount factors are equivalent to interest rates of 1, 5.23, 8.1, 11.1, 17.65, 25, and 42.86%. Results are shown only for the utility function $v_1 = 0.5 \ln (x - y)$ and several of the extreme values of the discount factor. The results using v_2 with any value of λ are nearly identical to those presented for v_1, and the graphs change uniformly with β, so the graphs in Fig. 2 represent the extreme changes.

Visually it is clear that the curves in Fig. 2 are extremely similar. For the discount factors $\beta - 0.99$ and $\beta = 0.70$ the optimal number of spawners to leave after harvesting agree at 50 out of 100 states and differ by only one grid point at the rest of the states. Moreover, it can be shown that this result remains valid for much finer grids; hence the two policies can be made to be extremely close together.

The long-run (ergodic) population sizes show a slight shift to smaller population sizes as β decreases, but the cumulative ergodic harvest distributions are virtually indistinguishable over the range of discount factors examined.

Figure 2(d) shows an optimal value function, $\sum_{t=1}^{t} \beta^{t-1} v_1(t)$ when starting in each state, for $\beta = 0.99$ and $\beta = 0.925$. Despite the fact that almost identical sample paths are generated by the two optimal harvesting strategies, the change in the valuation of the sample paths is dramatic.

There has been much discussion in the fisheries literature on the appropriate value of the discount factor (Walters 1975; Clark 1976; Walters and Hilborn 1976; Holling 1978). This discussion can be divided into two components—the discount factor that should be used to evaluate the fishery by an external agency such as a government agency (say to compare the benefits derived from a stream enhancement project) or a private individual (when making an entry decision, for example) and that used by the fishery manager to set policy, bearing in mind the effects harvest policy will have on the former decisions. If the previous empirical results are robust, they suggest that the fishery manager need not worry greatly about the exact choice of the discount factor used for determining policy, and that this choice will have little bearing on entry decisions or enhancement projects. This is because a nearly optimal expected present value will be found over a broad range of discount factors that might be used by the external agents.

Figure 3(a–e) shows similar results for the v_2 with $\beta = 0.95$ and $\lambda = 1.00$ and $\lambda = 0.05$. Runs were performed for $\lambda = 1, 0.95, 0.9, 0.8, 0.5, 0.25$, and 0.05 and for different values of β. The results were not sensitive to the particular value of β used. The results changed uniformly with λ; hence the curves for $\lambda = 1.00$ and $\lambda = 0.05$ represent the extreme curves found.

For $\lambda = 0.05$, more is harvested at lower population sizes, while less is harvested at larger population sizes.

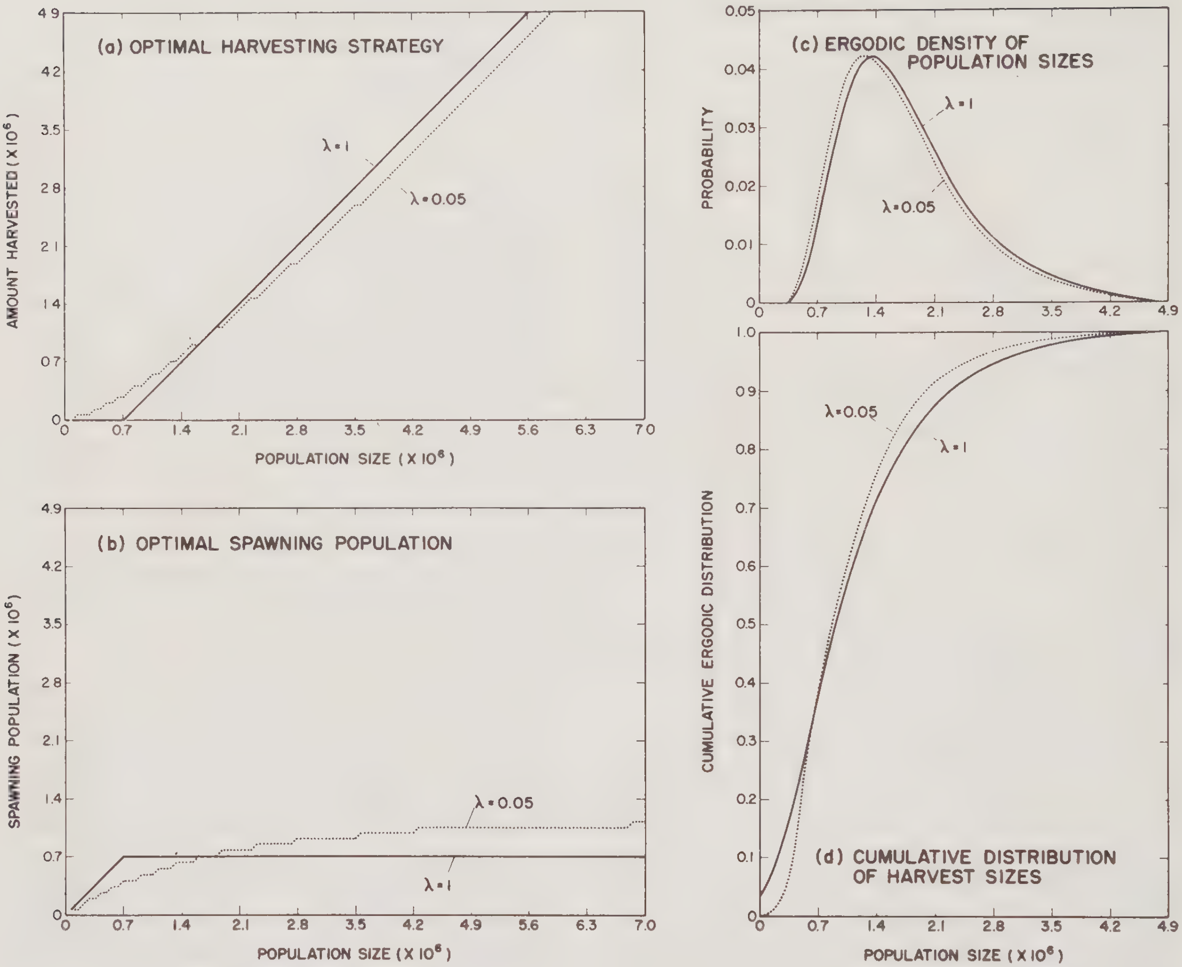

FIG. 3. Effects on an optimal policy and optimal value from varying the degree of risk aversion.

The crossover point is at a population size of 1.89×10^6, which is where (letting $\underline{d}$ denote the mean of d) the equation $\underline{d}4.082y \exp\{-0.8y\}$ has a value equal to $y = 1.89 \times 10^6$. Thus at the crossover point an individual just replaces itself in expectation.

Unlike the case for changes in β, the cumulative harvest distributions when λ varies differ by as much as 8%, and at the most probable harvest sizes, by about 5–6%. These differences are small but significant; the smaller values of λ can be seen to produce a "smoother" harvest in the long run.

These results can best be explained by considering the economic interpretation of the utility functions. At $\lambda = 1$, the price does not vary with supply (in fact it is $p = 1$, which can be viewed as the normalized price); therefore a harvest policy is based entirely on being as close as possible to the point of largest overall expected growth. However, at $\lambda = 0.05$, at low populations, the higher price (i.e. the higher risk) makes it desirable to harvest some now (i.e. the risk makes it desirable to obtain some amount of certain return now). At higher population levels, a balance must be maintained between a desirable price and future growth. For $y \geq 1.89 \times 10^6$, the expected value of x_{t+1} is less than y_t. Harvesting more now lowers the present marginal price per unit of fish, but increases the probability (i.e. decreases the risk) of larger population sizes next period (i.e. of small, unprofitable harvests next period).

The problem of unsmooth harvests from random populations is discussed in Mendelssohn (1976, 1980a, 1980b), Beddington and May (1977), and May et al. (1978). These empirical results suggest that unsmooth harvests have been found in the past because no effort has been made to include in management policies either attitudes towards risk, or marginal prices that are sensitive to supply. A reasonable conjecture is that all other things being equal, for a properly managed random fishery, wider fluctuations in catch will be expected either if outside supplies affect prices or if the entire quota cannot be taken by the fleet. Conversely, smaller fluctuations will be expected when the marginal price is very sensitive to the supply of the managed stock of fish only. Inventories can be viewed as an outside supply that affects

TABLE 1. Changes in relative risk aversion with changes in planning horizon length when following an optimal policy.

n	$\lambda = 1$	$\lambda = 0.5$	$\lambda = 0.05$
2	0.1430	0.0518	0.045
3	0.1684	0.303	0.423
4	0.1684	0.325	0.423
5	0.1684	0.331	0.423
6	0.1684	0.331	0.423
7	0.1684	0.331	0.423
8	0.1684	0.331	0.423
9	0.1684	0.331	0.423
10	0.1684	0.331	0.423

price, and they should have a very destablilizing effect if not taken into account in setting management policy for biologically random fisheries. This is precisely what has been seen in the salmon fishery in Alaska.

The solution of Eq. (2) offers some insights into relative risk aversion and planning horizons when optimal policies are followed. This is because Eq. (2) can be solved by solving the following sequence of recursive equations:

$$f_n(x) = \max_{0<y<x} \; g(x, y) + \beta E f_{n-1}(s[y, d])$$

where n denotes the number of periods remaining in the planning horizon. For Eq. (2), each $f_n(\bullet)$ is concave and continuous (Mendelssohn and Sobel 1980), and hence each is a risk averse utility. Each $f_n(x)$ is the utility of having x units of fish when there are n periods left when following *an optimal policy*. Hence $f_n'(x)$ is the marginal value of one additional unit of fish with n periods remaining, and the two risk averse measures R_1 and R_2 can be calculated as n changes (derivatives are approximated by finite differences) (Table 1). The measure R_2 reflects the relative risk aversion faced by the decision maker given the actual sample paths that will occur when following an optimal policy. What is noticeable is that the relative risk for f_n is much less than that for v_2, that it increases with n, and that it quickly becomes stationary after three to five periods. An optimal harvesting policy reduces the relative risk of the decision maker. Moreover, the effective planning horizon for these problems appears to be 3–5 yr, after which both policy, risk, and preferences remain stationary.

The measure of relative risk R_2 can be seen to be almost a measure of elasticity of the present marginal value of a unit of fish. As an optimal policy "smooths out" the supply of fish, the elasticity of the value per unit of fish decreases.

Conclusions

Any conclusions to be drawn from these results must be tempered by the realization that the results are derived from only limited numerical experimentation. However, the appendix presents theoretical results which suggest that over a broad class of stochastic harvesting models large changes in the discount factor produce only very small changes in an optimal harvesting policy. Hence, there is reason to believe the numerical results are in fact robust.

The numerical results suggest that policy often is insensitive to changes in the discount factor over a range of values likely to be found in practice. Discount factors may adequately represent intertemporal preferences for a dollar now versus an expected dollar in the future, but they do not seem to capture the attitude towards the degree of gamble in obtaining that expected dollar in the future.

Moreover, when the utility functions are viewed as total revenue curves with marginal price sensitive to supply, the results suggest that for optimally managed fisheries highly supply-sensitive prices will lead to stabilized harvests, whether the fishery is economically or biologically stochastic. As most if not all fisheries are stochastic, the usual assumption of perfect competition in fishery economic models and the lack of attention to risk preferences limit the usefulness of the results derived from these models.

External decisions for a fishery, such as entry decisions and enhancement projects, depend on the valuation of the fishery. The valuation of the fishery depends on the utility function used, the discount factor used, and the sample paths of the random harvest stream. Usually, the fishery manager can only control this last aspect through harvesting policy. The results of this paper suggest that under optimal management, misspecification of the discount factor in determining the optimal harvesting policy will have little effect on the external decisions of other parties.

Finally, as the degree of risk aversion increases, the amount harvested is not strictly nondecreasing for all population sizes. This seemingly is in contradiction with the results of Cropper (1976). The numerical results yield an intuitive explanation of why Cropper's result is not correct for this problem.

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Appendix

This appendix presents a rationale, but not a total proof, of why in a general setting policy, will change only slightly with changes in the discount factor. The notation and discussion follow Mendelssohn and Sobel (1980). The dynamic programming formulation of the optimal harvesting problem is

$$f(x) = \max_{y \in Y(x)} \{G(x, A(x)) + \beta E f(s[A(x), d])\}$$

For convenience, assume that an optimum always occurs at an interior point, which is true for one-period reward functions like ln $(x - y)$. Then the optimality conditions are

$$G^{[2]}(x, A(x)) + \beta E f'(s[A(x), d]) s^{[1]}[A(x), d] = 0$$

By substitution, this yields

$$G^{[2]}(x, A(x)) \\ + \beta E G^{[1]}(s[A(x), d], A(s[A(x), d])) s^{[1]}(A(x), d) = 0$$

For the specific case of $G(x, y) = (x - y)^\lambda$, this reduces to

$$\lambda(x - A(x))^{\lambda-1} + \beta E\{\lambda(s[A(x), d] \\ - A(s[A(x), d]))^{\lambda-1} s^{[1]}[A(x), d]\} = 0$$

or that

$$E\{\lambda(s[A(x), d] - A(s[A(x), d]))^{\lambda-1} s^{[1]}[A(x), d]\} \\ = \frac{\lambda(x - A(x))^{\lambda-1}}{\beta}$$

Suppose the discount factor is perturbed to $\beta + \delta$, such that $0 \leq \beta + \delta < 1$. Then at the value $A(x)$, the derivative has changed value by an amount

$$\frac{\delta\lambda(x - A(x))^{\lambda-1}}{\beta}$$

Let $\gamma = |\lambda - 1|$, then this is equivalent to

$$\frac{\delta\lambda}{\beta(x - A(x))^{\gamma}}$$

For example, for $\beta = 0.9$, $\lambda = 0.5$, and $\delta = -0.2$ (so that the new discount factor is 0.7), the resulting term is

$$\frac{-0.0111}{(x - A(x))^{1/2}}$$

so that the derivative is still almost zero at $A(x)$. Moreover, $s[\bullet, d]$ is concave, and an optimum is most often at values of y where $s^{[1]}[\bullet, d]$ changes rapidly. Hence, it requires very small changes in an optimal policy to account for even relatively large changes in the discount factor.

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An Iterative Aggregation Procedure for Markov Decision Processes

ROY MENDELSSOHN

National Marine Fisheries Service, NOAA, Honolulu, Hawaii

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An iterative aggregation procedure is described for solving large scale, finite state, finite action Markov decision processes (MDPs). At each iteration, an aggregate master problem and a sequence of smaller subproblems are solved. The weights used to form the aggregate master problem are based on the estimates from the previous iteration. Each subproblem is a finite state, finite action MDP with a reduced state space and unequal row sums. Global convergence of the algorithm is proven under very weak assumptions. The proof relates this technique to other iterative methods that have been suggested for general linear programs.

MOST REAL applications of Markov decision processes (MDPs) give rise to very large problems; this is particularly true if the state is represented as a vector of dimension greater than two or three. The major limitation to solving large scale MDPs appears to be in-core storage, as computers are now capable of performing iterations of algorithms for MDPs quickly. However, a 7-dimensional state with only 5 grid points per dimension would have 78,125 states and a transition matrix for each policy that could not be stored in present-day computers. In this paper, an iterative aggregation procedure is described for solving large scale MDPs which relieves this storage burden considerably.

The procedure to be described uses the linear programming (LP) formulation of a discounted MDP (d'Epenoux [1963]) and employs ideas for aggregation of LPs developed in Vakhutinskii and Dudkin [1973], Vakhutinskii et al. [1973, 1979], Agafanov and Makarova [1976], Zipkin [1977, 1980a, b], and Dudkin [1979]. In particular, for the special case of MDPs the procedure is an extension of Zipkin's weighted row and column aggregation of LPs (Zipkin [1977, 1980b]) with optimal disaggregation, and of the extensive Russian literature on iterative aggregation procedures for LPs (Vakhutinskii and Dudkin [1973], Vakhutinskii et al. [1973, 1979], Dudkin). At each iteration, the restrictions on how an aggregate problem may be formed are similar to those described in Thomas [1977] and Whitt [1978] for approximating MDPs.

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The major result of this paper is that if at each iteration the weights for aggregating the rows and columns of the LP are chosen properly, then the iterative procedure consisting of alternated aggregation and optimal disaggregation converges globally to an optimal primal and dual solution of the MDP. Convergence is proven using Zangwill's Convergence Theorem A ([1969], p. 19) for algorithms.

For MDPs, the results extend those of Zipkin [1980a] by showing how to iteratively choose the weights for weighted row and column aggregation, and by proving convergence of this procedure. Also, it is proven that for MDPs the LP described in Zipkin [1977] for optimal disaggregation can be reduced to a smaller MDP with unequal row sums (i.e., state and action dependent discount factors). This allows the subproblems to be solved by iterative techniques which are more efficient than linear programming.

The Russian literature on iterative aggregation procedures for LPs involves sequences of complicated unconstrained quadratic programming problems. Proofs of convergence (particularly global convergence), when they have been found (Dudkin, Vakhutinskii et al. [1979]), are complicated. The procedure presented in this paper was motivated by the realization that solving these quadratic programming problems is equivalent to one iteration of an exterior penalty function algorithm for solving (aggregate) LPs. When the quadratic programs (i.e., the exterior penalty functions) are solved as relaxed LPs many of the constraints are redundant. This yields a simpler iterative procedure and a stronger proof of convergence.

The major drawback of the procedure is that each revision of the row weights is equivalent to a dual variable update when using multiplier methods (Rockafellar [1973]), and requires the computational equivalent of one iteration of successive approximations on the full MDP. It is believed that the iterative aggregation process should converge more quickly for large problems than successive approximations on the original MDP. However, several alternative procedures are suggested for calculating the new row weights of each iteration requiring less computation but for which convergence is not proven.

1. THE MODEL

A Markov process is to be controlled over an infinite planning horizon. At the start of each period, a state i from a finite set of N states is observed, an action k is chosen from a finite set of K actions (where for convenience it is assumed the same K actions are available at each state), and a transition is made to state j at the start of the next period with probability $p(i, j{:}k)$.

In each period, if state i is observed and action k is selected, a cost

$c(i, k)$ is incurred. The cost in period t is discounted by a factor β^{t-1}, $0 \leq \beta < 1$, and it is desired to minimize the expected total cost over the infinite planning horizon. It is assumed that $c(i, k)$ is bounded (equivalently that $0 \leq c(i, k) < \infty$ for all i and k). It is well known (d'Epenoux) that a solution to this MDP can be found by solving the following linear programming problem (LP):

$$\text{Maximize } \textstyle\sum_{i=1}^{N} v(i)$$

$$\text{s.t. } \textstyle\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v(j) \leq c(i, k) \qquad (1.1)$$

$$\text{for} \quad i = 1, \cdots, N; \quad k = 1, \cdots, K$$

where

$$\delta_{ij} = \begin{cases} 0 & \text{if} \quad i \neq j \\ 1 & \text{if} \quad i = j \end{cases}.$$

Dual variables are denoted by $u(i, k)$, $i = 1, \cdots, N$; $k = 1, \cdots, K$, and let $v = \{v(i)\}$, $u = \{u(i, k)\}$. Opitmal primal and dual variables are denoted by $\bar{v} = \{\bar{v}(i)\}$ and $\bar{u} = \{\bar{u}(i, k)\}$.

In forming an aggregate problem attention is restricted to a reasonable subset of possible aggregations, similar to those described in Whitt. The idea is to form a reduced MDP with $N' \leq N$ aggregate states and $K' \leq K$ actions. In the LP formulation, each state has an associated column and each state-action pair has an associated row. Let σ be a partition of $\{1, 2, \cdots, N\}$ and let ρ be a partition of $\{1, 2, \cdots, K\}$. Let S_n, $n = 1, \cdots, N'$ be the nth subset of σ. Similarly, let A_l, $l = 1, \cdots, K'$ be the lth subset of ρ. Hence S_n references both the states and the associated columns that are aggregated into the nth state and column, and A_l references the actions and associated rows that are aggregated into the lth aggregate action and the associated (n, l)th row.

Following Dudkin, and Vakhutinskii et al. [1979], assume at the tth iteration estimates v^t, u^t for $\bar{v}$, $\bar{u}$ are given. Define the following aggregated terms (Zipkin [1980b]):

$$c^{t+1}(n, l) = (\textstyle\sum_{k\in A_l} \sum_{i\in S_n} c(i, k)u^t(i, k))/(\sum_{k\in A_l} \sum_{i\in S_n} u^t(i, k))$$

$$\text{for} \quad n = 1, \cdots, N'; \quad l = 1, \cdots, K'. \qquad (1.2a)$$

$$\hat{p}^{t+1}(i, m{:}k) = (\textstyle\sum_{j\in S_m} (\delta_{ij} - \beta p(i, j{:}k))v^t(j))/(\sum_{j\in S_m} v^t(j))$$

$$\text{for} \quad i = 1, \cdots, N; \quad m = 1, \cdots, N'; \quad k = 1, \cdots, K. \qquad (1.2b)$$

$$p^{t+1}(n, m{:}l) = (\textstyle\sum_{k\in A_l} \sum_{i\in S_n} \hat{p}^{t+1}(i, m{:}k)u^t(i, k))/$$

$$(\textstyle\sum_{k\in A_l} \sum_{i\in S_n} u^t(i, k)) \qquad (1.2c)$$

$$\text{for} \quad n = 1, \cdots, N'; \quad m = 1, \cdots, N'; \quad l = 1, \cdots, K'.$$

The aggregate terms in (1.2) are defined so as to ensure that for any subset of states either the states are totally aggregated (both across columns and across rows by actions) or else the states are not aggregated at all across either rows or columns. For notational convenience, it is assumed that the partitions do not change with each iteration. However, the proofs do not depend on this assumption, and some basis for choosing the partitions at each iteration is supplied by the algorithm.

Let $f_0(x)$, $f_i(x)$, $i = 1, \cdots, k$ be concave functions. For the problem: Max $f_0(x)$, s.t. $f_i(x) \leq 0$ for $i = 1, \cdots, k$, the Lagrangean $L(x, \lambda)$ is given by:

$$\begin{cases} f_0(x) + \sum_i \lambda_i f_i(x) & \text{if} \quad \lambda_i \geq 0 \quad \text{for} \quad i = 1, \cdots, k \\ \infty & \text{otherwise.} \end{cases}$$

Let $x^* = \text{argmax}_x\, L(x, \lambda)$ and $\lambda^* = \text{argmin}_\lambda\, L(x, \lambda)$. The well known result that $L(x^*, \lambda) \geq L(x^*, \lambda^*) \geq L(x, \lambda^*)$ is used in Theorem 2.2.

2. THE ALGORITHM AND ITS PROPERTIES

The iterative aggregation procedure is as follows. Choose any v^0, u^0 with $\infty > v^0 \geq 0$ and $\infty > u^0 \geq 0$. Assume that after iteration t, v^t and u^t are given.

Step (*i*). Form the aggregate coefficients defined in (1.2).

Step (*ii*). Solve the master program:

$$\text{Maximize} \sum_{n=1}^{N'} z(n)$$

$$\text{s.t.} \sum_{m=1}^{N'} p^{t+1}(n, m{:}l)z(m) \leq c^{t+1}(n, l) \tag{2.1a}$$

$$\text{for} \quad n = 1, \cdots, N' \quad \text{and} \quad l = 1, \cdots, K'.$$

Denote a primal solution to (2.1a) by $z^{t+1} = \{z^{t+1}(n)\}$, and the dual solution by $\lambda^{t+1} = \{\lambda^{t+1}(n, l)\}$.

Step (*iii*). Solve an LP for each $n = 1, \cdots, N'$:

$$\text{Maximize} \sum_{i \in S_n} v(i)$$

$$\text{s.t.} \sum_{j \in S_n} (\delta_{ij} - \beta p(i, j{:}k))v(j) \leq z^{t+1}(n)\hat{p}^{t+1}(i, n{:}k) \tag{2.1b}$$

$$\text{for} \quad i \in S_n \quad \text{and} \quad k = 1, \cdots, K.$$

Let v^{t+1} be the vector consisting of the optimal solutions to all of these problems, and denote the optimal dual variables by $\pi_n^{t+1}(i, k)$, where the subscript n denotes that $i \in S_n$.

Step (*iv*). Update the dual variables

$$\begin{aligned} u^{t+1}(i, k) = \{&(u^t(i, k)\lambda^{t+1}(n, l)/\textstyle\sum_{k \in A_l} \sum_{i \in S_n} u^t(i, k)) - (c(i, k) \\ &+ \beta \textstyle\sum_{j=1}^{N} p(i, j{:}k)v^{t+1}(j) - v^{t+1}(i))\}^+ \quad \text{for} \quad i \in S_n; \quad k \in A_l \end{aligned} \tag{2.2}$$

where $\{a\}^+ = \max(a, 0)$. Return to Step (i), or else stop if fixed point has been found.

Comment. The Russian literature (Vakhutinskii and Dudkin) also suggests updating the dual variables using the formula (similar but not identical to (2.2))

$$u^{t+1}(i, k) = (\lambda^{t+1}(n, l)/\textstyle\sum_{k\in A_l} \sum_{i\in S_n} u^t(i, k))\{u^t(i, k) \\ - (c(i, k) + \beta \textstyle\sum_{j=1}^{N} p(i, j{:}k)v^{t+1}(j) - v^{t+1}(i))\}^+.$$

A fixed point of the iterative process, if one exists, is denoted by v^*, u^*. The corresponding values of z, λ are denoted by z^*, λ^*. Note that the N' LPs (2.1b) have dual LPs that are Leontief (Koehler et al. [1975]), and hence can be solved by iterative techniques. Each such LP can also be viewed as an MDP with unequal row sums. The update (2.2) is a modification of the usual update in the method of multipliers.

It is conjectured that the dual LP to (2.1a) is also Leontief. This is true for the few small numerical examples solved to date using the algorithm.

An alternative to Step (iii) requiring less computational effort is fixed-weight disaggregation (Zipkin [1977; 1980a, b]):

$$v^{t+1}(i) = (v^t(i)z^{t+1}(n))/(\textstyle\sum_{j\in S_n} v^t(j)) \quad \text{for} \quad i \in S_n. \tag{2.3}$$

Similarly, Step (iv) can be replaced by a fixed-weight disaggregation:

$$u^{t+1}(i, k) = (u^t(i, k)\lambda^{t+1}(n, l))/(\textstyle\sum_{k\in A_l} \sum_{i\in S_n} u^t(i, k)) \\ \text{for} \quad i \in S_n; \quad k \in A_l \tag{2.4}$$

or, noting that Step (iii) of the algorithm yields a unique value of $\pi_n^{t+1}(i, k)$ for each (i, k):

$$u^{t+1}(i, k) = \pi_n^{t+1}(i, k). \tag{2.5}$$

Yet another alternative is "optimal disaggregation" (Zipkin [1977]), which finds a solution with higher objective value than (2.3):

$$\text{Maximize } \textstyle\sum_{i\in S_n} v(i)$$

$$\text{s.t. } \textstyle\sum_{j\in S_n} (\delta_{ij} - \beta p(i, j{:}k))v(j) \le z^{t+1}(n)\hat{p}^t(i, n{:}k) \\ \text{for} \quad i \in S_n; \quad k = 1, \cdots, K \tag{2.6a}$$

$$\textstyle\sum_{j\in S_n} (-\beta p(i, j{:}k))v(j) \le z^{t+1}(n)\hat{p}^t(i, n{:}k) \\ \text{for} \quad i \notin S_n; \quad k = 1, \cdots, K. \tag{2.6b}$$

Denote as before the optimal dual variables to (2.6a) as $\pi_n^{t+1}(i, k)$, and those of (2.6b) by $w_p^{t+1}(i, k)$, $p \neq n$. Before proving properties of the iterative algorithm procedure, it is necessary to prove that a solution to (2.1b) solves (2.6).

Lemma 2.1. *In the LP* (2.6), *none of the constraints* (2.6b) *are binding, that is* $w_p^{t+1}(i, k) \equiv 0$.

Proof. The dual LP to (2.6) has the following general form

$$\text{Minimize } \textstyle\sum_{i \in S_n} \sum_{k=1}^{K} \pi_n(i, k) h(i, k) + \sum_{i \notin S_n} \sum_{k=1}^{K} w_p(i, k) h(i, k)$$

$$\text{s.t. } \textstyle\sum_{j \in S_n} \sum_{k=1}^{K} (\delta_{ij} - \beta p(j, i{:}k)) \pi_n(i, k)$$

$$+ \textstyle\sum_{J \notin S_n} \sum_{k=1}^{K} (-\beta p(j, i{:}k)) w_p(i, k) = 1 \quad \text{for} \quad i \in S_n.$$

The dual LP is obviously Leontief. The lemma follows from Theorem 2.5.1 in Koehler et al.

The existence of an optimal solution to (1.1) has been well-established. The existence of a fixed point (v^*, u^*) for the iterative process will be proven by showing that (v^*, u^*) is a fixed point if and only if it is optimal in (1.1).

Theorem 2.1. (v^*, u^*) *is a fixed point of the iterative process described in Steps* (i)–(iv) *if and only if it is primal and dual optimal for* (1.1).

Proof. $(\bar{v}, \bar{u})$ *is a fixed point.*

The proof proceeds by showing that if $v^t = \bar{v}$, $u^t = \bar{u}$, then $z^{t+1}(n) = \sum_{i \in S_n} \bar{v}(i)$, and $\lambda^{t+1}(n, l) = \sum_{i \in S_n} \sum_{k \in A_l} \bar{u}(i, k)$. These values are optimal in the master problem if they are feasible and if they satisfy complementarity conditions. The latter is

$$\textstyle\sum_{n=1}^{N'} \sum_{l=1}^{K'} \{(\sum_{n=1}^{N} (\sum_{i \in S_n} \bar{v}(i)) \sum_{j \in S_n} (\delta_{ij} - \beta p(i, j{:}k))(\bar{v}(j)/\sum_{i \in S_n} \bar{v}(i))$$

$$- c(i, k))(\bar{u}(i, k)/\textstyle\sum_{i \in S_n} \sum_{k \in A_l} \bar{u}(i, k))\} (\sum_{i \in S_n} \sum_{k \in A_l} \bar{u}(i, k)) = 0.$$

After cancelling out terms, this reduces to:

$$\textstyle\sum_{i=1}^{N} \sum_{k=1}^{K} (\bar{v}(i) - (c(i, k) + \beta \sum_{j=1}^{N} p(i, j{:}k) \bar{v}(j))) \bar{u}(i, k) = 0$$

the complementarity condition for (1.1), which is true by assumption. Since $\bar{v}$, $\bar{u}$ are primal and dual feasible, positive weighted sums of the rows and columns cannot change this. Hence $z^{t+1}(n) = \sum_{i \in S_n} \bar{v}(i)$ and $\lambda^{t+1}(n, l) = \sum_{i \in S_n} \sum_{k \in A_l} \bar{u}(i, k)$ are primal and dual feasible in the master problem.

Depending on how the partitions are chosen, $\lambda^{t+1}(n, l) = \sum_{i \in S_n} \sum_{k \in A_l} \bar{u}(i, k)$ may be positive for more than N' values of (n, l). However, at $z^{t+1}(n) = \sum_{i \in S_n} \bar{v}(i)$, the (n, l)th constraint in (2.1a) becomes:

$$(1/\textstyle\sum_{k \in A_l} \sum_{j \in S_n} \bar{u}(i, k)) \sum_{k \in A_l} \sum_{j \in S_n} \bar{u}(i, k)$$

$$\cdot [\textstyle\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k)) \bar{v}(j) - c(i, k)] \leq 0$$

which from the optimality of $(\bar{v}, \bar{u})$ holds with equality for each (n, l). The master LP hence has possibly degenerate optimal solutions. The values $\lambda^{t+1}(n, l) = \sum_{i\in S_n} \sum_{k\in A_l} \bar{u}(i, k)$ in practice can be found by finding all possible optimal solutions to (2.1a).

Using the LP form of Step (iii) given in (2.6), it is evident that $v^{t+1} = \bar{v}$. Since $\bar{v}$ is feasible and optimal, the second term on the right-hand side of (2.2) is always nonpositive. The first term reduces to $\bar{u}(i, k)$. If $\bar{u}(i, k)$ is zero, then the brackets imply $\bar{u}^{t+1}(i, k) = 0 = \bar{u}(i, k)$. If $\bar{u}(i, k) > 0$, then

$$c(i, k) + \beta \sum_{j=1}^{N} p(i, j{:}k)\bar{v}(j) - \bar{v}(i) = 0, \quad \text{so again} \quad u^{t+1}(i, k) = \bar{u}(i, k).$$

(v^*, u^*) *is optimal in* (1.1).

(v^*, u^*) is optimal in (1.1) if v^* is primal feasible, u^* is dual feasible and (v^*, u^*) satisfies the complementarity conditions. As (v^*, u^*) is a fixed point by assumption, then $z^*(n) = \sum_{i\in S_n} v^*(i)$, $\lambda^*(n, l) = \sum_{i\in S_n} \sum_{k\in A_l} u^*(i, k)$. From (2.2), v^* is feasible in (1.1) or else u^* would not be a fixed point.

As above, writing out the complementarity conditions for the master problem (2.1a) at (z^*, λ^*) and substituting in their values yields:

$$\sum_{i=1}^{N} \sum_{k=1}^{K} (v^*(i) - (c(i, k) + \beta \sum_{j=1}^{N} p(i, j{:}k)v^*(j)))u^*(i, k) = 0$$

so (v^*, u^*) indeed satisfies the complementarity condition.

At $\lambda^*(n, l) = \sum_{i\in S_n} \sum_{k\in A_l} u^*(i, k)$, (2.2) becomes

$$u^*(i, k) = (u^*(i, k) - (c(i, k) + \beta \sum_{j=1}^{N} p(i, j{:}k)v^*(j) - v^*(i)))^+$$

which is the usual dual update for the method of multipliers. As $u^*(i, k)$ is invariant at v^*, it follows from Rockafellar that u^* is dual optimal.

It is shown in Zipkin [1977] that "optimal" weightings should be proportional to optimal values. A theorem similar to Theorem 2.1 is proven in Vakhutinskii et al. [1979]. The possible degeneracy of the master LP (2.1a) suggests that at each iteration, partitions should be chosen such that $\sum_{k\in A_l} \sum_{j\in S_n} u^t(i, k) > 0$ for only one l for each $n = 1, \cdots, N'$. In this case, the algorithm reduces to an aggregation procedure for policy evaluation, and a multiplier type step for policy improvement. Otherwise, partitions should be chosen such that the dual constraint matrix is Leontief.

Theorem 2.2 states the main results of this paper, that under very weak conditions the iterative aggregation procedure converges to a solution of (1.1). Note that the iterative aggregation procedure can be viewed as a point to set map A: $R_+^N \times R_+^{N\times K} \to R_+^N \times R_+^{N\times K}$. The theorem is proven by showing that the algorithm satisfies the conditions of Zangwill's Theorem A (Zangwill [1969]).

THEOREM 2.2. *Assume for* $(v^0, u^0) > 0$ *that* v^1, u^1 *are nonnegative and bounded when one iteration of the procedure is performed. Let* $\{(v^t, u^t)\}_{t=1}^{\infty}$ *be the sequence of vectors generated by the algorithm. Then* *either* $\{(v^t, u^t)\}$ *converges to* $(\bar{v}, \bar{u})$ *or else there is a convergent subsequence with* $(\bar{v}, \bar{u})$ *as the limit of the subsequence.*

Proof. It is necessary to show that A is an upper semicontinuous point to set map defined on a compact set, and that there exists some function that changes monotonically with each iteration of the algorithm.

(i) *The penalty function.*

$$x(v^t) = \textstyle\sum_{i=1}^{N} v^t(i) - 1/e \sum_{i=1}^{N} \sum_{k=1}^{N} ([\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k)]^+)^2$$

monotonically decreases with t *for some fixed value* $e > 0$.

Remark. This result relates iterative aggregation for MDPs to the iterative algorithm for nonaggregated linear programs proposed in Mangasarian [1979].

Bertsekas [1975] has shown that there exists for linear programs an exact penalty function method such that for all e in the interval $(0, \bar{e})$, the penalty function algorithm converges. Let e be one such value. Using (2.2), the Lagrangean function for the master problem (2.1a) at iteration $t + 1$ can be written as

$$\begin{aligned}
\text{Maximize } &\textstyle\sum_{n=1}^{N'} z(n) - \sum_{n=1}^{N'} \sum_{k=1}^{K'} w(n, l) \\
&\cdot \{\textstyle\sum_{k\in A_l} \sum_{i\in S_n} ((\lambda^t(n, l)u^{t-1}(i, k)/\sum_{k\in A_l} \sum_{i\in S_n} u^{t-1}(i, k)) \\
&+ \textstyle\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k))^+ \\
&\cdot (\textstyle\sum_{n=1}^{N'} z(n) \sum_{j\in S_n} (\delta_{ij} - \beta p(i, j{:}k))(v^t(j)/\sum_{j\in S_n} v^t(j)) - c(i, k))\}.
\end{aligned} \tag{2.8}$$

At $w(n, l) \equiv 1/e$ and at the trial value $z(n) = \sum_{i\in S_n} v^t(i)$, (2.8) reduces to:

$$\begin{aligned}
&\textstyle\sum_{i=1}^{N} v^t(i) - (1/e) \sum_{n=1}^{N'} \sum_{l=1}^{K'} \{\sum_{k\in A_l} \sum_{i\in S_n} ((\lambda^t(n, l)u^{t-1}(i, k)/ \\
&\quad \textstyle\sum_{k\in A_l} \sum_{i\in S_n} u^{t-1}(i, k)) + \sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k))^+ \\
&\qquad \cdot (\textstyle\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k))\}.
\end{aligned} \tag{2.9}$$

At iteration t, let I^- denote the set of (i, k) such that (2.2) is nonpositive, and I^+ the set of (i, k) such that (2.2) is positive. Then (2.9) can be rewritten as:

$$\begin{aligned}
&\textstyle\sum_{j=1}^{N} v^t(i) - (1/e) \sum_{n=1}^{N'} \sum_{l=1}^{K'} \{\sum_{k\in A_l} \sum_{i\in S_n} (\lambda^t(n, l)u^{t-1}(i, k)/ \\
&\quad \textstyle\sum_{k\in A_l} \sum_{i\in S_n} u^{t-1}(i, k))(\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k))\} \\
&\quad - (1/e) \textstyle\sum_{(i,k)\in I^+} (\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k))^2 \\
&\quad + (1/e) \textstyle\sum_{(i,k)\in I^-} \lambda^t(n, l)u^{t-1}(i, k)/\sum_{k\in A_l} \sum_{i\in S_n} u^{t-1}(i, k) \\
&\qquad \cdot (\textstyle\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k)).
\end{aligned} \tag{2.10}$$

If in the second term of (2.10),

$$(\textstyle\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k))$$

were replaced by

$$\textstyle\sum_{n=1}^{N'} (\sum_{j\in S_n} (\delta_{ij} - \beta p(i, u{:}k))z^t(n)(v^{t-1}(j)/\sum_{j\in S_n} v^{t-1}(j))) - c(i, k)$$

then from the optimality of $z^t(n)$, $\lambda^t(n, l)$ in (2.1a), the entire term would be zero. However, (2.1b) ensures that

$$\begin{aligned}&\textstyle\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j)\\ &\qquad \le \textstyle\sum_{n=1}^{N'} (\sum_{j\in S_n} (\delta_{ij} - \beta p(i, j{:}k))(z^t(n)v^{t-1}(j)/\sum_{j\in S_n} v^{t-1}(j)))\end{aligned}$$

and that their respective weighted sums (over $k \in A_l$, $i \in S_n$), weighted by

$$(\lambda^t(n, l)u^{t-1}(i, k))/(\textstyle\sum_{k\in A_l} \sum_{i\in S_n} u^{t-1}(i, k)),$$

are identical. Hence the second term in (2.10) is still identically zero. For $(i, k) \in I^-$, by definition

$$\textstyle\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k) \le 0,$$

hence

$$\begin{aligned}&(\lambda^t(n, l)u^{t-1}(n, l))/(\textstyle\sum_{k\in A_l} \sum_{i\in S_n} u^{t-1}(n, l))\\ &\qquad\qquad \cdot (\textstyle\sum_{j=1}^{N} (\delta_{ij} - \beta p(i, j{:}k))v^t(j) - c(i, k)) \le 0.\end{aligned}$$

These two results imply that (2.10) is less than or equal to $x(v^t)$.

Moreover, this implies for $w(n, l) \equiv 1/e$, $\max_z L(z, w)$ occurs at $z(n) = \sum_{i\in S_n} v^t(i)$. Therefore $L(z^{t+1}, \lambda^{t+1}) \le L(z^{t+1}, 1/e) \le L(z^t, 1/e) \le x(v^t)$. The optimality of z^{t+1}, λ^{t+1} in the master LP (2.1a) and the fact that v^{t+1} solves the N' problems (2.1b) guarantee that the penalty function evaluated at v^{t+1} is less than or equal to $L(z^{t+1}, \lambda^{t+1})$.

(ii) *The sequence* $\{v^t, u^t\}$ *is bounded.*

By assumption, $x(v^1)$ is finite, and from part (i) of the proof, $x(v^t)$ is nonincreasing with t, so the sequence $\{v^t, u^t\}$ is bounded above. Straightforward algebra proves that the penalty function for (2.1) evaluated at z^t provides a lower bound for $x(v^t)$. Since z^t is optimal in (2.1) at iteration t, $x(v^t) \ge 0$. By definition, $u^t \ge 0$. Together, these facts imply $\{v^t, u^t\}$ is bounded from below.

(iii) *The point to set map A is upper semicontinuous* (*closed*).

Since the partitions are the same each iteration, there exists three constant matrices $T^1((N'K') \times 1))$, $T^2(1 \times N')$, and $T^3(NK \times N)$ such that the constraints for the master problem in Step (i) can be written

$$(T^1u')T^3(vT^2) \leq (T^1u')c.$$

As the mapping is linear and continuous, and the constraint defines a convex set, the mapping A^1 is closed. Zangwill [1969] proves that the maximization operator is closed; call this A^2. Similarly, the constraints for the subproblems form closed maps, call them A^3, A^4, $\cdots$, $A^{N'+2}$, and Equation 2.2 is trivially closed, call this map A^0. Therefore the map A can be written as $A = A^0A^2A^{N'+2} \cdots A^2A^3A^2A^1$. The assumption that (v^1, u^1) is finite guarantees that the algorithm produces a sequence of bounded vectors, that is, A is defined on a compact set. Closedness of A then follows from Corollary 4.2.1 in Zangwill ([1969], p. 96).

(iv) *The algorithm converges to a fixed point.*

That the algorithm converges follows from Theorem A in Zangwill [1969]. To show that it converges to a fixed point, the algorithm maps the sequence $\{v^t, u^t\}_{t=0}^{\infty}$ into the sequence $\{v^t, u^t\}_{t=1}^{\infty}$. Two subsequences of a convergent sequence on a compact set have the same limit point. Denote it by (v^*, u^*). However,

$$(v^*, u^*) = \lim_{t\rightarrow\infty} A: (v^t, u^t) = A(v^*, u^*)$$

the final equality following from A being a closed map.

When Steps (i)–(iv) of the iterative aggregation process are used only every kth iteration, and the alternatives (2.3), (2.4), or (2.5) are used at all other iterations, proofs of convergence follow closely the proof of Theorem 2.2 to derive the conditions necessary for Zangwill's other convergence theorems. Intuitively, either a fixed point is found, or else every kth iteration of the algorithm, the equivalent of one iteration of successive approximations is calculated. As long as the intermediate steps do not force the value function v and the dual variables u in undesirable directions, the algorithm converges since successive approximations converge when applied to MDPs.

Finally, it is conjectured that convergence can be proven in an analogous manner to Theorem 2.2 if only some subset of the dual variables are adjusted by Equation 2.2 at each iteration. (This is in the spirit of several relaxation algorithms (Agmon [1954], Motzkin and Schoenberg [1954]).) For example, one partition at a time could be updated each iteration using Equation 2.2.

Theorem 2.2 can also be proven using the augmented Lagrangean in part (iii) instead of the penalty function. As the dual update (2.2) is a method of multipliers update, the algorithm approximates the maximum v for each u^{t+1} in the augmented Lagrangean. Sufficient conditions for such approximate procedures to converge are given in Rockafellar.

Clearly the algorithm need not be run until it converges if approximate solutions are satisfactory. Since at the end of each iteration $\pi_n{}^t$ describes a nonrandomized policy that can be followed, any of the bounds for aggregate LPs or MDPs given in Whitt, Zipkin [1980b], and Mendelssohn [1980] can be used as stopping rules.

3. CONCLUSION

An iterative aggregation procedure for MDPs has been presented which converges globally to an optimal value function and to optimal dual variables. The process requires less in-core storage at any point than does solving the full MDP. However, each iteration requires at least the computational equivalent of one iteration of successive approximations. Convergence should be more rapid using the iterative aggregation process.

To reduce the computational burden, several alternative procedures are presented at key steps. Convergence has not been proven when these procedures are used; however, if the full iterative aggregation process is used every kth iteration, then again the algorithm converges globally.

There should exist a more efficient computational method for updating the dual variables at each iteration, a method which converges globally. Improvements in this area should lead to truly efficient means for solving large-scale MDPs.

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Annex H

Report of the Sub-Committee on Small Cetaceans

1. PARTICIPANTS, AGENDA AND INTRODUCTORY REMARKS

The meeting was chaired and the meeting report edited by Perrin. Members (M) of the Scientific Committee of the IWC and invited experts (E) attending all or part of the sessions were: Anderson (M), Balcomb (E), Braham (M), Brodie (M), Choi (M), Christensen (M), Dahlheim (E), Duguy (E), Finley (M), Fleischer (M), Gong (M), Hammond (E), Hay (M), Ivashin (M), Jarrell (M), Kapel (M), Kato (M), Klinowska (M), Leatherwood (E), Mitchell (M), Ohsumi (M), Øritsland (M), Wada (M), and Walker (E).

The draft agenda was discussed and approved with amendments (Appendix 1). Leatherwood and Walker were appointed as rapporteurs. Subgroups were convened and chaired as follows: abundance and stock assessments, Hammond; vital rates, Anderson; catch statistics, Dahlheim; and pollution and industrial development, Klinowska.

Due to time constraints it was agreed to concentrate on white whales, narwhals and killer whales and to simply highlight new information and problems on others. In addition to its usual charge, the sub-committee was asked to respond to a request to the Scientific Committee from Canada for scientific advice on five aspects of exploited white whale and narwhal populations within the extended fishing zone of Canada: (a) present stock sizes, initial stock sizes and present carrying capacity if considered different from initial; (b) replacement yields and sustainable yields, with comments if they are markedly different; (c) nature of assessments and comments on their general reliability; (d) 5-year or longer projections of the stock sizes given a continuation of current harvest levels; and (e) any other relevant infomation.

2. DOCUMENTATION

Documents available to the sub-committee and containing information on small cetaceans were SC/33/Prog Reps Australia, Brazil, Canada, Chile, Denmark (Greenland), France, Iceland, Japan, Korea, Mexico, New Zealand, Norway, Peru, South Africa, Spain, UK, USA and USSR; SC/33/Rep 4; IWC/33/11A–E; SC/33/SM2–4, 6, 8–11; SC/33/O 4, O 6 and O 8–O 12; and issues LXXXV and LXXXVI and the provisional issue LXXXVII of the International Whaling Statistics. Documents submitted to the sub-committee are listed in Appendix 2.

3. REVIEW OF NEW INFORMATION ON STOCKS, CATCHES AND STATUS

All takes of small cetaceans by IWC members for which statistics were available for the meeting are listed in Appendix 3. They total 112,006 dolphins, porpoises and small whales. Discussion was limited to species for which there is new significant information bearing on stock assessment and management.

3.1 Northern bottlenose whale

There was no new information available.

3.2 White whale

The distribution of the white whale is characterised by a disjunct circumpolar range with distinct concentrations occupying traditional, non-overlapping summering areas (IWC, 1980). These discrete groups are recognised as management units, or stocks, some of which are defined on the basis of morphometric differences, mainly in body size (Sergeant and Brodie, 1969; SC/33/SM9), and on responses (declines) of populations under hunting pressure without apparent recruitment from adjacent populations (Mitchell and Reeves, 1981; SC/33/SM9).

3.2.1 Distribution, migration, identity of stocks and abundance

(a) The Bering – Chukchi – Mackenzie area and Cook Inlet

Unpublished material cited in SC/33/SM9 indicates a population of 6–7,000 white whales in the Beaufort-Mackenzie Delta area. No new information was provided on other areas. The sub-committee again urges that studies be conducted to provide information on stock discreteness and on levels of take for the stock(s).

(b) Barents, Kara, White and Okhotsk Seas

SC/33/SM2 provided further evidence for the claim of Ognetov (1981) that the populations of the White, Barents and Kara Seas are all from one stock. Counts of animals in the White Sea ranged from a low of 232 in 1979 to a high of 1,570 in 1971 and were negatively correlated to severity of ice conditions in the Kara and Barents Seas. The information provided in 1980 and this year on the relation between White and Kara Sea white whales differs from previously published morphometric studies (Sergeant and Brodie, 1969). The new analyses indicate that whales from the two areas are not morphologically different. The sub-committee recommends that: (a) the Soviet data used by Sergeant and Brodie be compared with recent morphometric data (Ognetov, 1981) and that both sets be examined for any source of bias, and (b) if biases are absent or similar for the two data sets they be combined and re-analysed.

There is no new information on the Sea of Okhotsk population.

(c) Davis Strait – Baffin Bay, Cumberland Sound, and Hudson Bay – Ungava Bay

An estimate from aerial survey of 8,940 white whales wintering in Hudson Strait and Ungava Bay (SC/33/SM9) was regarded by the sub-committee as reasonable, though a probable under-estimate of the population. There was concern about the probability of duplicate counts, under-estimates and differences between counts from the two sides of the survey aircraft. It was recommended that, if possible, data be re-analysed, treating the two available transect sets or other strata as replicates to produce separate estimates, to provide information on variability.

Estimates were presented (SC/33/SM9) showing that white whales from western Hudson Bay, eastern Hudson Bay, and Ungava Bay over-winter together in pack ice in Hudson Strait. These animals separate in spring and migrate to their distinct, non-overlapping summering areas. Based on two pieces of evidence, these three groups should be considered separate stocks as defined above. First, the population levels of each stock have behaved independently, with little or no migration between regions. The West Hudson Bay stock has remained relatively stable at high numbers, while the other two stocks have separately suffered drastic declines due to heavy hunting. Second, the group have begun their summer migrations and are separated by the time of calving and calf-rearing (late May).

A further differentiation of these three stocks in the aggregate from that of Cumberland Sound has been made on morphometric grounds (SC/33/SM9).

The current and historic abundance of Canadian stocks and areas are given in Table 1.

3.2.2 *Catches*

The recent catches of white whales by Canada, Denmark and the USSR are presented in Tables 1 and 2. For selected stocks, Table 1 includes most recent catch figures and the rate of exploitation these catches represent.

3.2.3 *Hunting loss rate*

New information on loss rate was contained in SC/33/SM9. Losses in eastern Hudson Bay are minimal, because the whales are harpooned before they are shot and because the hunt takes place in clear, shallow water. In 1980 the sub-committee cited estimates of 20–60%, with higher values for deeper water (Seaman and Burns, 1981: 571). Because this problem is an important one for small stocks that are being harvested and for those stocks for which we have no reliable population size estimates, it is recommended that research on loss rates be carried out on white whales like that conducted on narwhals (SC/33/SM10).

3.2.4 *Status*

The sub-committee's consideration of status of stocks centred on new information available on populations in Hudson Bay and northern Quebec. It was noted that three stocks were severely depleted and continue to be exploited at high rates. The eastern Hudson Bay stock is estimated at less than 10% of original size, Ungava Bay at less than 20% of original, and Cumberland Sound at 12–14% of original (Table 1). The sub-committee concluded that these stocks should each be designated as a Protected Stock with zero catch.

The stock in the High Arctic in eastern Canada and western Greenland and that in the Beaufort Sea – Mackenzie River delta are at relatively high levels of abundance, and catches are relatively low. However, Canadian catch statistics are not complete, and the USA has not reported catch levels from the Beaufort Sea.

Little is known about stocks in the Bering and Chukchi Seas, the Barents – Kara – White Sea and Cook Inlet. The sub-committee recommends that the USA and USSR conduct research to determine identity of stocks, population sizes, and current exploitation rates.

3.2.5 *Age determination and vital rates*

There is valuable new information available on age determination. Results for several workers (Table 3) indicate that tooth reading techniques are comparable among them. Growth data for a captive animal support the hypothesis of two growth layer groups. (GLGs . . . terminology of Perrin and Myrick, 1980) per year (SC/33/SM7) and the sub-committee believes the hypothesis should be accepted on a provisional basis for the white whale.

Table 1

Historical and current abundance of currently exploited white whale stocks in Canada and Greenland. Unless otherwise noted, data are from SC/33/SM9 (A) or SC/33/ProgRep Canada (B)

	W. Hudson Bay	E. Hudson Bay	Ungava Bay	Cumberland Sound	High Arctic	Beaufort – Mackenzie
Historical	10,000 (Sergeant, 1973)	as many as 5,000 (A)	⩾1,000 (A)	5,000 (Mitchell and Reeves, 1981)	—	—
Current	8–9,000 (A)[1]	< 500 (A)[4]	< 200 (A)[4]	600–700 (SC/32/SM17)	10–20,000 (A)	6–7,000 (A)
% of original	80–90%	< 10%	< 20%	12%	—	—
1980 Quota	—	—	—	40 (B)	—	—
1980 Take	251[2] (B)	156 (1979) (B)[2]	88 (1979) (B)[2]	43 (B)	567[2] (B) and SC/33/ProgRep Denmark	85 (B)[3]
1980 Take as % current population	2.8–3.1%	> 31%	> 44%	6–7%	2.8–5.6%	1–1.5%

[1] Extrapolated from proportion of total numbers estimated in Hudson Strait which were thought attributable to W. Hudson Bay stock(s).
[2] Canadian catch figures not complete.
[3] Western Canada only, does not include Alaskan catch; Canadian catch figures not complete.
[4] Finley clarification of several figures used in SC/33/SM9.

Table 2

Available catch data for white whales in Canada, Greenland, and the USSR 1976–1980[1] (from SC/33/ProgRep Canada, SC/29, 30, 32, 33/ProgRep Denmark, Seaman and Burns, 1981 and Ivashin and Mineev, 1981).

	USSR					Canada[2]				Greenland		
	Vessel	Land-based				Canadian Arctic		Hudson Bay				
	White, Barents and Kara Seas	Gulf of Yenisey	White Sea	Barents Sea	Bering Sea	Eastern	Western	Eastern[3]	Western	Reported catch	Est. total catch	USA Reported catch
1976		170	302	38	21	239	154	546	146	1,059	1,200	—
1977	457	64	215		29	286	148	682	191	690	800	247
1978		19			32	161	127	297	118	519	600	177
1979		74	179		26	200	144	319	105	526	700	138
1980	60	81	75		20	133	85		124	264	550	—
Totals	517	408	771	38	128	1,019	658	1,844	684	3,058	3,850	562

[1] Grouping of catch by geographic area does not imply definition of stock.

[2] Canadian data are not complete because of incomplete reports from some villages and individual hunters.

[3] Catches from James and Ungava Bays and Northern Quebec are included with Eastern Hudson Bay.

Potential utility of other methods was discussed. Ageing based on assumed calving interval and count of ovarian scars is not possible because of high and variable corpora counts. Comparison of most recently deposited layers in teeth from animals caught at different seasons should be made. Such material is available or readily obtainable. Rates of racemization in aspartic acid of the eye lens nucleus could be determined from material currently available (Bada *et al.*, 1980).

Table 3

Estimated number of dentinal layers (GLGs) and age, assuming two GLGs/year, at attainment of sexual maturity

	Brodie (1971)		Sergeant (1973)		SC/33/SM9	
	GLGs	Age	GLGs	Age	GLGs	Age
Males	>14	>7	16–18	6.8	17–21	7.5–10.5
Females	9–11	4.5–5.5	8–13	4–6.5	11–13	5.5–6.5

3.2.6 Net reproductive rates and sustainable yields

After lengthy discussions, the sub-committee concluded that there is no good basis for estimating net reproductive rates in white whale populations. Estimates of gross annual reproductive rates exist (on the order of 10–12%—Anon., 1980), but data that would allow estimation of natural mortality rates are not available. A Leslie-matrix approach to very crudely approximate average adult natural mortality rate was considered for application to the body of age-frequency data in Sergeant (1973), but this proved not useful because the data do not conform to the assumption of constant mortality rate over the period represented.

Two estimates of sustainable yields do exist. Brodie *et al.* (1981) cited crude birth rates of 12–14% in the western Hudson Bay stock and estimated replacement yield for the Cumberland Sound stock by subtracting 4.5% natural mortality (by analogy with the long-finned pilot whale—Sergeant, 1962) from 12%, yielding 5% as 'surplus production'. This calculation was the basis for the quota of 40 whales that Canada internally set for 1980. Members of the group agreed that there is insufficient basis to suppose that natural mortality rates are the same in white whales as in pilot whales. Pilot whales are apparently later-maturing and longer-lived than white whales (age determination discussed above for white whale and in Sergeant (1962) for long-finned pilot whale) and may have different breeding systems, suggesting that the two species may have quite different mortality rates.

The second estimate of sustainable yield is that of Sergeant (1981), who regarded the 1949–1968 catch of white whales at Churchill, Seal River, and Whale Cove (all on western Hudson Bay) as 'nearly in balance with this population's natural increase'. He continued, 'if this is so, it follows that an annual catch of about 5% . . . would not be excessive'. However, the members of the sub-committee feel that this conclusion is questionable on several grounds, to wit:

(1) because there are no data on size of the population before the aerial survey of 1965, the rate of decline in abundance is unknown;

(2) there is no published evidence for the existence of a 'resident' stock said to be represented in 10% of the catches; and

(3) the decline in annual catch, 1951–68, and the decline in modal length of males in the catch (in spite of bonuses paid for larger animals) are indicative of exploitation of an unknown and not necessarily 'moderate' degree.

For these reasons, and pending further investigation of the catch history and status of the western Hudson Bay stock, the sub-committee believes that the 5% figure should definitely not be used as a 'rule-of-thumb' estimate of sustainable yield for white whale populations.

The group discussed and wishes to stress the importance of determining the way gross production may change with population density in the white whale. The sub-committee re-iterates the need for more comparative studies of calf ratios in greatly reduced stocks, such as the eastern Hudson Bay stock (estimated to be at 7% of original size) with those in stocks that may be closer to original size, such as the Cook Inlet or Lancaster Sound stocks. Because of the wide variation in water clarity and in behaviour in different areas, efforts should be given to developing methods for standardizing calf counts through quantifying sighting and behavioural conditions. Because of the selectivity inherent in existing fisheries, there is little hope of being able to estimate natural mortality rates through analysis of catch data.

The sub-committee also wishes to stress that the various estimates cited above, and below in the narwhal discussion, are for the most part point-estimates or ranges of point-estimates, they do not incorporate estimates of statistical variability. As such, they are very crude and should be considered as provisional only, pending availability of more extensive data sets that allow more sophisticated statistical treatment.

With respect to maximum sustainable yield, the sub-committee notes that current thinking is that in long-lived, probably K-selected large mammals (having low litter size and extended parental care) such as odontocetes, MSY level is most likely significantly higher than 50% of initial population size; that is, density-dependent responses to changes in population size are non-linear (for example, see Smith, 1979). Given the severely depleted status of the Cumberland Sound, Ungava Bay and eastern Hudson Bay stocks of white whales, and if it be assumed that reproduction increases with decreased density, it is certain that maximum sustainable yields for those stocks are greater than the current replacement yields. This suggests that a programme of provisional complete protection could result in significantly greater harvests in the long term.

3.3 Narwhal

3.3.1 Distribution, migration, identity of stocks and abundance

No new documents were available on distribution or stock identity. There is persuasive evidence for existence of one main stock in the Canadian Arctic, West Greenland and North Greenland (Mitchell and Reeves, 1981). Finley and Brodie reported, however, that there are frequent catches from northwestern Hudson Bay and that wintering animals may be found in eastern Hudson Strait. These two groups may belong to a smaller, separate stock that summers in northern and western Hudson Bay and winters in Hudson Strait as described for white whales (SC/33/SM9).

Kapel and Finley reported that aerial surveys were carried out in March-April 1981 in southern Baffin Bay – northern Davis Strait as well as in the Hudson Strait – southern Hudson Bay area, and that results are expected to be presented at next year's meeting. Narwhals were found widely distributed in cracks and holes in the pack-ice throughout Baffin Bay – Davis Strait.

Reported catches in recent years are presented in Table 4.

3.3.2. Catches

The actual take is probably more than reported. Although Canadian regulations require all landed narwhals, male and female, to be tagged, harvest statistics do not include lost or abandoned carcasses or unreported animals (SC/33/ProgRep Canada). In addition, kills of females are not likely to be reported (tagged), in order to reserve available tag quotas for tusked males (SC/33/SM10).

3.3.3 Hunting loss rates

In 1980 the sub-committee cited an estimate of loss rate of 50% (Mitchell and Reeves, 1981). Additional information presented in SC/33/SM10 indicates that loss rates can be variable, depending on the type of hunt and ice conditions. For example, in 1978 an ice ridge afforded hunters an elevation providing a good firing angle for inflicting fatal injuries (and high losses) at the ice edge hunt for narwhals. In 1979 there was no similar vantage point, and there appeared to be few losses, although many narwhals received superficial wounds. Such circumstances explain the high rate (23–42%) of scarring found on the landed catch of narwhals from northern Baffin Island.

3.3.4 Status

No new information was available concerning status.

3.3.5 Age determination and vital rates

New data on ageing presented by Hay (1980) indicated that based on length-frequency analysis, three layers may be deposited in dentine and mandibular bone in the first two or three years of life. If accumulation rates of corpora albicantia based on annual ovulation rate are correct, adult females may deposit one layer per year. The workshop did not resolve the question of annual deposit of one or two layers (Hay, 1980).

Finley and Miller (SC/33/SM10) found that males were about 390 cm long (with 100 cm tusks) and females about 340 cm long at sexual maturity. Hay (1980) reported similar values, with dentinal-layer counts of 17 for males and approximately 12 for females. Estimates of age at first reproduction will depend on the rate at which dentinal layers are actually accumulated.

Accurate estimates of pregnancy rate, birth rate, calving ratio and natural mortality were not available, and there are very few data on population structure. Seven of 18 mature females examined by Finley and Miller

Table 4

Available catch data for narwhals in Canada and Greenland 1976–80.
(From SC/33/ProgReps Canada, Denmark, SC/32/ProgRep Denmark, SC/30/ProgReps 29, 30, 32 and 33)

	Canada		Greenland		Totals
Year	Western Hudson Bay	N.E. Canadian Arctic	Reported catch	Estimated catch	(Canada and Greenland est.)
1976	8	297	106	110[1]	415
1977	8	200	232	350	558
1978	4	275	503	650	929
1979	30	289	289	350	669
1980	25+	325	185	350	700+
Totals	75+	1,386	1,315	1,810	3,271+

[1] Exclusive of Thule and East Greenland.

(SC/33/SM10) were pregnant, a similar ratio to that found by Hay. In a group of narwhals trapped in a *savssat,* there were 25 calves for 50 adult females (SC/32/ProgRep Canada). The representativeness of the sample is questioned because the group contained few adult males, and the degree to which females and calves segregate or concentrate is unknown. If it is assumed that adult males escaped from the *savssat* and that the original sex ratio was 1:1, then the proportion of calves would have been 19.2% of total.

3.3.5 Net reproductive rate and sustainable yield

As is the case for the white whale (discussed above), there were no data or analyses available to the sub-committee that would allow estimation of natural mortality rate. Therefore estimation of net reproductive rate and replacement and sustainable yields is not possible. The same problems and comments discussed above for the white whale apply here for the narwhal, including the inadvisability of using the 5% figure promulgated by Sergeant (1981) for use for the narwhal (by analogy with the white whale).

As discussed above, the very long history of substantial catches and the present estimates of abundance suggest that the narwhal population is not in a crisis situation such as are the three heavily depleted white whale stocks, and present takes may be smaller than replacement yields. However, in view of the fact that recent data indicate that narwhal takes on the coast of Greenland and those in the Canadian High Arctic are probably from the same stock (IWC, 1980, 1981), research should be continued to more accurately and completely document the take and to collect survey data and comprehensive biological data and specimens that will allow more precise estimation of the size and composition of the population than is possible with existing data. The sub-committee looks forward to the release of the results of the recent aerial survey of the narwhal wintering grounds in the Davis Strait carried out by Canada.

3.4 Killer whale

3.4.1 Review of report of workshop

The sub-committee reviewed and discussed the report of the Workshop on Identity, Structure and Vital Rates of Killer Whale Populations (SC/33/Rep 4). The workshop noted that while killer whales may be found in nearly every area of the world's oceans, concentrations are mainly near coasts and in high latitudes. Morphometrics and colouration may be useful tools in defining some types of geographical or ice-edge/open-water forms, but existing evidence of a high degree of isolation over a few hundred miles for coastal animals in coastal waters of the eastern North Pacific suggests that broader-scale stock areas as used for larger species may be inappropriate for killer whales. Given the extreme stability of local populations and the possibly low reproductive rates evidenced by the available data, any exploitation can be expected to have very long-term impacts on population size and structure.

Among the recommendations for research, the Workshop proposed that (1) reports be solicited from researchers to determine if social and breeding structure is similar to that in the eastern North Pacific; (2) osteological material in public museums and institutions useful for studies of age and of morphological variation be inventoried and their study encouraged and (3) studies be continued of animals in the wild to accurately determine life-history parameters.

3.4.2 The Northeast Atlantic Fishery

There is no new information on stock identification, abundance or migrations. SC/Jn81/KW1 reported year-round occurrence in Norwegian coastal waters, with 3 or 4 areas of particular concentration. Suggestions that the whales move in response to prey movements (Jonsgård and Lyshoel, 1970 and others) require further investigation.

Based on a long catch history, the killer whales in the eastern North Atlantic in 1980 were recommended to be provisionally classified as a Sustained Management Stock pending review this year of information necessary for identification of stocks and assessment of their status (*Rep. int. Whal. Commn* 31). In 1980, Norway voluntarily limited catch to 52 animals.

Christensen stated that mean lengths (SC/Jn81/KW1) have not changed appreciably from those previously reported (Jonsgård and Lyshoel, 1970).

The statement in SC/33/Rep4 that no new data have been received is incorrect (SC/Jn81/KW1). However, the available data are still inadequate for stock assessment.

3.4.3 The Southern Hemisphere fishery

3.4.3.1 Identity and status of stocks

Information available to the sub-committee from the workshop is still inadequate to define stocks for management. Data and analyses are inconclusive with respect to the six to eight longitudinally-defined stocks proposed by Mikhalev *et al.* (1981). There are data on other possible divisions. Description of a 'dwarf' form by Mikhalev *et al.* (1981) indicates that two species or subspecies may exist in the Southern Hemisphere. Ongoing work by Berzin and Vladimirov (SC/Jn81/KW11) may confirm existence of morphologically distinct forms in open waters and at the ice-edge. Colouration studies indicate a similar division (SC/Jn81/KW11). Analysis and stratification of the sample of killer whales taken by the USSR in 1979/80 may help to clarify the situation, but at the present no identification of separate stocks can be made.

3.4.3.2 Abundance

Data from 1978/79 and 1979/80 IDCR cruises were compared with Japanese sightings data by five-degree square, and an estimate of a Southern Hemisphere population of 144,900 killer whales was arrived at (SC/Jn81/KW10). A correction for differences in survey area produced a revised estimate of 254,000 (Appendix 4), but the methods are subject to several critical untested assumptions. Particularly, density within the five-degree-square strata is assumed to be homogeneous. Concern was expressed that effort directed along the ice edge and at minke whale concentrations may be biased towards areas of high killer whale density within some five-degree squares. If so, this could cause an overestimation of density within these strata. The effect of earlier Japanese sighting effort directed at sei whale concentrations before 1970 is unknown.

Hammond plans to re-examine available data on density of killer whales, taking into account 1980/81 IDCR data. The sub-committee requests of the Secretariat that data from the 1980/81, earlier and subsequent IDCR cruises be verified and made available for analysis before next year's meeting.

Lacking a basis for delineating stocks, there is no basis for catch limits. Pending more research of the type done elsewhere on population structure and stock identity, the sub-committee concluded that there should be no catches of killer whales in the Southern Hemisphere.

3.4.3.3 Catches

There were no catches of Antarctic killer whales in the 1980/81 season.

3.4.3.4 Sustainable yields

Sustainable yields cannot be estimated until vital rates are better known, stocks are delimited, and adequate population assessments are conducted.

3.5 Pilot whales

Small catches of long-finned pilot whales were noted for Greenland (SC/33/ProgRep Denmark) and Canada (SC/33/ProgRep Canada). SC/33/O 4 presents an abundance estimate from aerial survey data of populations of pilot whales in the Newfoundland – Labrador Area of 13,167 (± 3,155) whales. The take of 2,773 in the Faroe Islands (provisional issue LXXXVII of the International Whaling Statistics) represented a considerable increase over the 1979 catch of 1,725 (IWC, 1981: 153). The sub-committee is concerned that there is no population estimate for the Faroes and apparently no scientific programme documenting composition of the catches. Accordingly, the sub-committee urges that Denmark be requested to supplement current reports with improved accounting of catch composition.

Takes of short-finned pilot whales off Japan were also higher in 1980 (692—SC/33/ProgRep Japan) than in 1979 (104—IWC, 1981: 153). It was unclear whether the 1980 figure represents an increase in takes or simply a better reporting system. Balcomb reported that annual takes fluctuate but that in the 1975 drive fishery in Taiji alone 500–600 animals were havested. Fifty-three were reported taken that year in Japanese small-type whaling (Issue LXXXV of the International Whaling Statistics). Noting that there is fishing for pilot whales in Japan in small-type whaling and drive fisheries, the sub-committee encourages implementation of a by-village reporting system and a summary of historical fishing effort, abundance and composition of catches.

Short-finned pilot whales are also taken on the West Indian Islands of St Vincent, St Lucia and Dominica. In 1978 there were eight boats equipped to hunt for pilot whales (five in Castries, three in Vieux Fort). Walker reported that information from fishermen at that time indicated that catches were low, probably below 50 animals per year. He also reported that the fishery on St Vincent continues to decline; 1980 catches from two boats were probably around 11 animals.

3.6 Other Small Cetaceans

3.6.1 Bottlenose Dolphin

The reported Japanese take of 3,493 (SC/33/ProgRep Japan) represents a substantial increase over the 1979 take of 666 (IWC, 1981: 153). The sub-committee is concerned over the increased take, particularly since there is no estimate of population size and no data available on composition of the catch.

3.6.2 Striped Dolphin

The sub-committee noted with concern that the reported catch of striped dolphins in the drive-in fisheries in Shizuoka and Wakayama Prefectures, Japan, increased greatly in 1980. The total take for Japan was 16,344 (SC/33/ProgRep Japan); in 1979 it was only 2,193 (IWC, 1981: 153). Kasuya (1976) estimated total population size in 1974 at 186–202,000, less than 50% of the estimated original population of more than 404,000. He estimated MSY at 4,140–6,530 and replacement yield at slightly less. As pointed out in the 1980 report of the sub-committee, Kasuya's estimates were based on assumptions and models that need further examination. No new stock assessment has been carried out as recommended, even though available new estimates of life-history parameters could well strongly affect the outcome of a re-assessment. In any case, the take of over 16,000 is three to four times the estimated sustainable yield.

Ohsumi reported that the drive fisheries do not require a license and that the dolphin populations are not managed. He also reported that responsibility for local fisheries rests with the prefectural governments, not with the national government directly.

The sub-committee is extremely concerned about this severe over-exploitation of the striped dolphin population, which spends only part of the year in Japanese waters. There is a clear need for re-assessment of the populations of this and other species taken in the drive fisheries and for management of the stocks on a scientific basis.

3.6.3 Common Dolphin

Information presented in SC/33/SM11, supplemented by information provided by Duguy, documents a harpoon fishery for dolphins along the Atlantic coast of France which may take over 200 dolphins per year (*Delphinus delphis* and *Stenella coeruleoalba*).

3.6.4 Dall's Porpoise

Ohsumi reported that the figure of 1,000 Dall's porpoise captured incidentally in the salmon drift-net factory ship operation in the North Pacific (see Section 5) (SC/33/ProgRep Japan) is the *reported* catch, which is lower than the actual catch because of a misunderstanding of the reporting requirements by the fishermen. The USA (SC/33/ProgRep USA) estimated that 8,970 Dall's porpoise were taken within the US 200-mile limit off the Aleutian Islands during the summer of 1980. That figure is listed in Appendix 3.

3.6.5 Harbour Porpoise

Previous statements that records of strandings of harbour porpoise on the British Coast have declined (Evans, 1980; Sheldrick, 1976) have been taken to support contentions of population declines. New analysis of the same stranding data presented in SC/33/SM4 do not support those statements of strandings trends, noting instead significant fluctuations in reported strandings between 1936 and 1949.

A new programme has begun to monitor incidental kills of harbour porpoise in Pasamaquoddy Bay, between Maine and New Brunswick (SC/33/ProgRep USA).

4. STATISTICAL REPORTING FOR LIVE-CAPTURE FISHERIES

The sub-committee discussed live-capture fisheries, and members agreed that statistics for these removals from the populations should be reported to the Scientific Committee as are those for other types of directed take. Live capture of dusky dolphins is reported in SC/33/ProgRep South Africa, but known take by the USA of bottlenose dolphins and by Iceland of killer whales has not been reported to the Scientific Committee. Bryant (1981) listed live captures of 30 killer whales in Iceland during the period 1975–79. The sub-committee urges that members be requested to provide live-capture statistics.

5. INTERACTIONS BETWEEN SMALL CETACEANS AND FISHERIES

5.1 Incidental take

Incidental takes are listed in Appendix 4. Discussion was limited to new developments, summarised below by geographical region.

5.1.1 Europe

The sub-committee notes that incidental takes of small cetaceans have not been reported to the Scientific Committee by the United Kingdom, although contaminant analyses of incidentally-caught harbour porpoise have been reported in an ICES document (see 6 below).

Duguy (SC/33/SM11) reported that small cetaceans are taken incidentally in trawl and gillnet fisheries on the Atlantic coast of France, including long-finned pilot whales, striped dolphins, bottlenose dolphins, common dolphins, Risso's dolphins and harbour porpoises. He also reported that a system exists for mandatory reporting of incidental kills. Noting that France has not included such existing information in the Progress Report, the sub-committee believes that this should be done, for both the Atlantic and the Mediterranean coasts.

5.1.2 North America

The sub-committee reviewed information on progress of the joint US-Japan research programme on the problem of incidental kill of Dall's porpoise in the salmon gillnet fishery near the Aleutian Islands (SC/33/ProgRep USA). The estimated kill in 1980 was 8,970. Abundance has been estimated variously at 840,000 to 2,300,000 but it is thought that these may be overestimates because of several biases. Joint sighting cruises to collect more and better data on distribution and abundance continue. Stomach-contents analyses show that prey items taken by the porpoise are on the average larger and deeper-living than those utilised by salmon.

Balcomb reported that incidental mortality of harbour porpoise occurs in the US gillnet fishery in the Puget Sound area of the state of Washington. He collected 23 dead porpoise assumed to have been killed in gillnets in 1972. The sub-committee notes that the mortality in this fishery has not been reported in the US Progress Report.

A reported 254 dolphins and porpoise were killed in fishing gear on the southeastern coast of Newfoundland (SC/33/PS13: p. 22 and Table 5). Many of the entrapped animals were used as food. This count was extrapolated to an overall estimate for Newfoundland of 23,399. The estimate was based on a telephone poll of 100 fishermen asked to keep records of their incidental catch. It is pointed out in SC/33/PS13 that the estimate may not be accurate because the sample was from one part of the coast of Newfoundland but was used to extrapolate to the entire coast. Hay reported that the large majority of the 254 animals in the reported sample were taken by a few fishermen in one location and that most of the fishermen reported no catch. He stated that in his recollection the telephone survey was retrospective.

This information indicates that significant incidental catches of small cetaceans may be occurring off Newfoundland, and the sub-committee urges that Canada be requested to collect and report accurate and precise statistics.

5.1.3 South America

Perrin reported that he has learned of incidental takes of tucuxi (*Sotalia fluviatilis*) and boutu (*Inia geoffrensis*) in gillnet and seine fisheries for catfish (*Brachyplatostoma* spp.) in the Amazon River. Da Rocha has indicated that statistics for these incidental takes will be included in Brazil's Progress Report next year.

The sub-committee notes that Argentina, Chile and Peru have not reported takes for fisheries in which incidental kill of small cetaceans is known to occur (IWC, 1980).

5.1.4 Asia

Gong reported that small cetaceans of several species are taken incidentally in mackerel purse seines in southern waters of the Republic of Korea. Fishermen will be notified shortly of a new requirement that incidental capture be avoided and that live captured animals be released. Incidental take resulting in death of the animal must be reported to the fisheries agency. Statistics of incidental catch will be included in next year's Progress Report.

5.1.5 South Pacific

The sub-committee notes that SC/33/ProgRep New Zealand for this year includes information and statistics on incidental catch of small cetaceans in fishing gear. The species involved are dusky dolphin, common dolphin, Hector's dolphin and long-finned pilot whale.

5.1.6 Eastern Tropical Pacific

The UK reported incidental catch of spotted, spinner and other small cetaceans by tuna seiners registered in the Cayman Islands.

Hammond reported that several IWC members that are known to operate purse seine vessels fishing for tuna associated with dolphins in the eastern tropical Pacific are not at present participating in the international programme of research conducted by the IATTC on the problem. The programme includes placement of observers aboard purse seiners to collect incidental catch statistics and data and specimens for use in assessing status of the dolphin populations. The non-participating members include the Republic of Korea, Mexico, the Netherlands (Netherlands Antilles), Spain and the UK (Cayman Islands).

Fleischer reported that while Mexico is not participating in the international effort, a programme of research on the problem is being planned, including placement of observers on vessels and preparation of an identification guide for use by Mexican fishermen. It is not planned to collect sightings and effort, but no decision has been reached on collection of biological specimens. A report on the progress of the research programme will be included in next year's Progress Report.

Recent analyses have uncovered several potential biases in life-history data collected from dolphins killed in the fishery (SC/33/SM6), throwing earlier estimates of life-history parameters into doubt. Perrin reported that research to cope with these biases is underway.

The sub-committee notes that the estimated incidental kills in 1980 of both spotted and spinner dolphins increased about 100% over those in 1979 (SC/33/SM3). Kill of common dolphins decreased about a third. It was pointed out that the large changes in the extrapolated estimates may merely reflect the large variances caused by the small sample size of non-US vessels. The sub-committee wishes to emphasise that it is very important that more IWC members participate in the IATTC programme, so that better estimates can be obtained. The sub-committee also urges that the status of the dolphin stocks be assessed and that results of analyses and assessments be made available to the Scientific Committee.

5.1.7 Eastern Tropical Atlantic

A recent newsletter on West African marine mammal research (Maigret, 1981) contains information on dolphin mortality in tuna seines off West Africa. Seven French seiner captains (23% of those asked) made on the average less than 12 sets on dolphins annually, killing about 14 dolphins per set.

Maigret extrapolated from this sample to arrive at an estimate of 3,300 dolphins killed annually, based on the fleet of about 42 seiners from France, 12 from the USA and 14 from Spain that fished off West Africa in 1977/78. Incidental kill of dolphins in this fishery had not been reported to the Scientific Committee by these IWC members, and the sub-committee believes they should be requested to do so.

Maigret (1981) also reported incidental kill of common dolphins in a surface trawl fishery for sardines, mackerel and '*chinchards*'. In May, 1980, one trawler captured 6 to 22 common dolphins per haul during trawling at night. Twelve vessels from Romania and the USSR were fishing by this method in the area at this time. The sub-committee notes that incidental kill statistics for this fishery have not been reported to the Scientific Committee.

5.2 Direct conflicts

New information was available on interaction between killer whales and a drop-line fishery in waters off Tasmania (SC/33/ProgRep Australia). An initial estimate is that approximately 10% of the catch of blue-eyed trevalla (*Hyperoglyphe porosa*, Centrolophidae) may be lost to killer whales. Further work on the interaction is planned.

The report of the killer whale workshop (SC/33/Rep4) contains information on take of halibut off longlines by killer whales off Iceland.

5.3 Competition

Ohsumi and Kato reported on progress of research on the problem of perceived competition between fishermen and dolphins at Iki Island, Nagasaki Prefecture, Japan. A team of scientists was recently assembled to conduct ecological research. A programme of research lasting at least three years is planned. The research includes analysis of dolphin stomach contents. Research on methods to drive the dolphins away from fishery areas continues.

Ohsumi reported that present plans are to submit a preliminary report on the results of the research to next year's meeting of the Scientific Committee.

6. EFFECTS OF POLLUTION AND INDUSTRIAL DEVELOPMENT

6.1 New information on pollution

The sub-committee reviewed the IWC observer's report on a joint session of the ICES Marine Environmental Quality and Marine Mammals Committees (IWC/33/11A). Two papers related to small cetaceans were presented. Analysis for lead, cadmium, and mercury in 26 harbour porpoise from the northeast coast of Scotland revealed a trend towards increasing residues of mercury and cadmium with increasing body length in some tissues (ICES Paper E.41[1]). However, data points were sufficiently scattered that no statistical relationship could be shown. Concentrations of lead were below detection limit for all samples. Based on these results and the supposed migratory habits of harbour porpoise as they affect results of such studies, the authors suggested that the harbour porpoise may not be acceptable as an index species for monitoring metal concentrations in the marine environment.

In a second report, levels of mercury and organochlorine residues in two white whales from the St Lawrence estuary were compared with those from other areas. An adult female, found dead of an old injury, contained 36.9 ppm mercury in the liver (ICES Paper E.55[1]). High levels of both total DDT and PCB's were found in this whale and in a healthy calf killed by hunters, but the calf had five times as much total DDT and 25 to 35 times as much PCB as the adult. Unfortunately, neither paper reported any anatomical or histological information.

The sub-committee reiterates its support for the view expressed by ICES that studies of pollutants should not only deal with amounts but also with effects, and that anatomical and histological information should be included in reports so that possible confounding effects of infections, etc., may be made clear. The efforts of ICES to standardise assay techniques were noted.

No full reports relating to small cetaceans were available to the sub-committee. Two harbour porpoise were collected for heavy metal and organochloride analysis under Canadian government permit (SC/33/ProgRep Canada). A study of skin ulcerations in marine mammals (SC/33/ProgRep France) and the analysis of samples from stranded specimens for heavy metal and pesticide residues (SC/33/ProgRep New Zealand) were reported. The latter material includes that from a mass stranding of killer whales and from the bottlenose dolphin and common dolphin. Document SC/33/ProgRep Spain refers to a study of organochloride contamination in a Blainville's beaked whale. Duguy added that a study of 34 small cetaceans relating to organochloride residues will be presented at the next ICES meeting.

6.2 New information on industrial development

Document SC/33/ProgRep Canada lists a working paper on the reactions of whales to boat traffic in the area of the confluence of the Saguenay and St Lawrence rivers, an area where small cetaceans are found. Scientists of 2 nations contributed to and participated in a workshop on underwater noise generated by super tankers and its possible effects on marine mammal populations in Arctic waters (SC/33/ProgRep Denmark and ProgRep Canada). The question of noise effects on marine mammals was raised at the sub-committee meeting last year (IWC, 1980).

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[1] At authors' requests, these Publications presented to ICES were unavailable for release or complete citation.

The proceedings of the workshop will be submitted for public review. The US reports that environmental impact statements are in preparation relating to the occurrence of marine mammals in or near oil lease sites in the Gulf of Alaska (SC/33/ProgRep United States).

7. OTHER BUSINESS

7.1 Publication of documents

Documents intended for publication in the Report are so indicated in Appendix 2. Authors will obtain reviews by at least 2 peers and send revised versions for publication to the Scientific Editor by 1 October 1981.

7.2 Reproduction Conference

Note was taken of the Conference on Cetacean Reproduction, to be held 28 November to 7 December 1981 in La Jolla, California, USA. The symposium of the conference has a full programme of 52 papers; these and others submitted (for circulation only) before the conference will be considered for publication in a proceedings volume. A workshop that will follow the symposium is fully subscribed. The workshop is designed to bring biologists and quantitative workers together for interchange of ideas on the limits and possibilities of work on reproductive biology of cetaceans.

7.3 Conference on tropical Atlantic cetaceans

The sub-committee recognises and encourages current plans for a conference on the cetaceans of tropical West Africa and suggests that the scope of the meeting be expanded to include cetaceans of the tropical western Atlantic as well. The organiser of the conference is J. Maigret, Editor of GEMMATA (Newsletter of Groupe d'Etude des Mammifères Marins dans l'Atlantique Tropical Africain). Persons interested in the meeting should contact Dr J. Maigret at Centre National de Recherches Océanographiques et de Pêches, BP22, Nouadhibou, R. I. de Mauritanie.

7.4 Grant to IWC by the Netherlands

The Government of the Netherlands had contributed Df. 10,000 to the IWC Research Fund with the suggestion that it be spent 'on such activities as may be recommended by the Scientific Committee with regard to the conservation of small cetaceans'.

After discussion of possible uses of the grant, the sub-committee concluded that in light of problems of stock identification of killer whales in Norwegian waters, Norway should be invited to prepare a research plan for the utilisation of the grant for field studies to identify killer whale stocks on the Norwegian coast. Photographic and acoustic survey would seem to be the most promising methods for this work.

7.5 CITES

The sub-committee noted that the volume 'A World Review of the Cetacea' has been published. The volume was financed by the Nature Conservancy Council of the UK and authored by M. Klinowska. Klinowska and Rudge thanked the members of the sub-committee for their help in preparing the volume. The sub-committee hopes that this useful compilation will be updated by the authors at regular intervals.

7.6 Terminology

The sub-committee noted the recent re-description of the clymene dolphin, *Stenella clymene*, based on examination of extensive materials from widespread tropical Atlantic locations (Perrin *et al.*, 1981). The species is valid and should be added to the IWC list of cetacean names.

8. RECOMMENDATIONS TO THE SCIENTIFIC COMMITTEE

8.1 Northern bottlenose whale

The sub-committee again recommends that the research programme recommended for the northern bottlenose whale in 1977–78 be carried out and that the stock continue to be classified a Protection Stock with a zero catch.

8.2 White whales and narwhals

(1) The sub-committee notes that the status of most small cetaceans in the IWC remains unresolved and that a resolution adopted at the 1980 meeting of the Commission (*Rep. int. Whal. Commn* 31: Appendix 8) established an interim working arrangement for continuation of the work of the sub-committee and provision of scientific advice to the member governments. The resolution also calls for provision of data and analyses to the Scientific Committee by member governments. The sub-committee recognises that advice promulgated under the present working arrangement has resulted in expansion of national research programmes on some species and adoption of voluntary internal catch limits for some stocks. Nonetheless, the sub-committee believes that for scientific reasons the white whale and narwhal should be managed on the same basis as the other Arctic whales. Commonalities affecting scientific management are several, including long migrations, subsistence take of individual animals by indigenous peoples using light craft and harpoons (with various modifications from modern technology), relatively high loss rates that must be measured, and quantifiable fishery effort. For these reasons, most of the members of the sub-committee recommend that the white whale and narwhal be listed in the Schedule (Paragraph 1) and that stock classifications and catch limits be set in accordance with the Commission's management procedures. The two whales should be listed thus:

> 'white whale' (*Delphinapterus leucas*) means any whale known as white whale, beluga, belukha
>
> 'narwhal' (*Monodon monoceros*) means any whale known as narwhal, sea unicorn

Ivashin expressed the opinion that this recommendation is inappropriate in light of last year's resolution of the Commission.

(2) The sub-committee notes the responsive and considerable expansion of studies of populations of white whales and narwhals in Canadian and Greenland waters and recommends that Canada and Denmark be encouraged to continue this very important work, giving particular attention to stock identity (including identification of discrete summering populations), migration, abundance, calf production, collection of complete and accurate catch statistics, and full collection of age and reproductive samples from the catch.

(3) Noting the seriously depleted status of the stocks summering in Cumberland Sound (estimated to be at less than 14% of original size), Ungava Bay (less than 20% of original) and eastern Hudson Bay (less than 10% of

original) and the importance to the species of estuarine calf-rearing grounds, the sub-committee recommends that each of these separate stocks be classified as a Protected Stock with zero catch, and that critical habitat of the stocks be recommended for protection.

(4) Noting that the problems of unknown stock structure, abundance and status identified by this sub-committee in 1979 and 1980 for populations of white whales summering in US and Soviet Arctic waters remain for the most part unresolved, the sub-committee recommends that the US and the USSR be urged to initiate field studies needed for stock identification and assessment. Noting that the USA did not submit white whale catch statistics for 1980, it is recommended that it be asked to do so.

8.3 Killer whales

The sub-committee endorses the detailed recommendations of the Workshop on killer whale populations (SC/33/Rep 4) and includes the most important of them here.

8.3.1 Norway

(1) The Committee last year recommended that because of a long history of catches the killer whales in the northeastern Atlantic be classified provisionally as a Sustained Management Stock, pending review of identity and status of stock(s) at this year's meeting. Data necessary to establish identity and assess status of the stock(s) are still not available. In addition, the catch data and new information on the size and nature of stocks elsewhere indicate that the recent takes on the northern coast of Norway may have come from one or a few localized stocks rather than from an overall northeastern Atlantic stock. For these reasons, the sub-committee recommends that the killer whales on the coast of Norway be designated an Unclassified Stock with zero catch limit, pending identification of stocks and assessment of their status.

(2) Noting that data exist on sex and length of catches since 1938, the sub-committee recommends that catch data be analysed as planned by Norway with consideration of possible biases in capture, to determine whether changes in length frequency or sex composition have occurred.

(3) Because available effort data are inadequate for CPUE analyses, the sub-committee recommends that should the fishery continue, improved reporting of effort be requested from the fishermen. Such reports should include at least: time leaving port, time returning to port and estimated time searching.

(4) Noting that acoustic and photographic enumeration techniques have produced highly successful results in defining killer whale populations in other areas, the sub-committee recommends that such techniques be considered for use in delineating the Norwegian stock(s).

(5) Because of the perceived competition between fishermen and killer whales for herring, the sub-committee recommends that, should the fishery continue and whenever possible, stomach contents be examined by scientists and both species composition and volume determined.

(6) Noting the success of short-term censuses in inland marine waters of British Columbia and Washington, the sub-committee recommends that the planned whale count in coastal waters of Norway be carried out.

8.3.2 Antarctic

(1) Because of the continuing uncertainty over stock identities and consequently the abundance of any Southern Hemisphere stocks, the sub-committee recommends that the stock(s) be classified as an Initial Management Stock with a catch limit of zero.

(2) Noting the large amount of information on stock (or 'community') identity yielded by extended photographic and acoustic surveys in the northeastern Pacific, the sub-committee recommends that these and other methods be considered for use in expanded field studies to delineate Southern Hemisphere populations.

(3) Noting that a large sample (916) of killer whales was taken in 1979/80 by the USSR and has not yet been fully reported on, the sub-committee recommends that the USSR be requested to provide suitable report(s) to next year's meeting of the Scientific Committee. The report(s) should include analysis of reproductive data and specimens collected, analysis of morphometric, meristic and colour-pattern data, exact locations of catches, sightings-and-catch per effort data, and information on hunting strategy and tactics, especially as they may relate to possible sex, age or size bias in the samples from the catch and to possible biases in sighting effort. If possible, samples for morphological analyses should be stratified by age.

8.4 Statistics

As pointed out in previous years, catch statistics provided to the Scientific Committee or to BIWS by member nations are incomplete or inadequately detailed. The sub-committee again recommends that member nations be requested to collect and submit full statistics as detailed in *Rep. int. Whal. Commn* 30: 124. Member nations known to have taken small cetaceans but which did not report the takes or reported them incompletely include Argentina (Incidental), Australia (I), Brazil (I), Canada (Directed and I), Chile (I), France (D, I), Iceland (Live-capture), Republic of Korea (I), Mexico (I), Netherlands (I), Peru (I), Spain (I), UK (I), USA (D, I, L) and USSR (I).

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Appendix 1

AGENDA

1. Participants, agenda and introductory remarks.
2. Documentation.
3. Review of new information on stocks, catches and status.
    - 3.1 Northern bottlenose whale.
    - 3.2 White whale.
        - 3.2.1 Distribution, migration, identity of stocks and abundance.
        - 3.2.2 Catches.
        - 3.2.3 Hunting loss rates.
        - 3.2.4 Status.
        - 3.2.5 Age determination and vital rates.
        - 3.2.6 Net reproductive rates and sustainable yields.
    - 3.3 Narwhal.
        - 3.3.1 Distribution, migration, identity of stocks, and abundance.
        - 3.3.2 Catches.
        - 3.3.3 Hunting loss rates.
        - 3.3.4 Status.
        - 3.3.5 Age determination and vital rates.
        - 3.3.6 Net reproductive rates and sustainable yields.
    - 3.4 Killer whale.
        - 3.4.1 Review of report of workshop.
        - 3.4.2 The Northeast Atlantic fishery.
        - 3.4.3 The Southern Hemisphere fishery.
    - 3.5 Pilot whales.
    - 3.6 Other small cetaceans.
        - 3.6.1 Bottlenose dolphin.
        - 3.6.2 Striped dolphin.
        - 3.6.3 Common dolphin.
        - 3.6.4 Dall's porpoise.
        - 3.6.5 Harbour porpoise.
4. Statistical reporting for live-capture fisheries.
5. Interactions between small cetaceans and fisheries.
    - 5.1 Incidental take.
        - 5.1.1 Europe.
        - 5.1.2 North America.
        - 5.1.3 South America.
        - 5.1.4 Asia.
        - 5.1.5 South Pacific.
        - 5.1.6 Eastern tropical Pacific.
        - 5.1.7 Eastern tropical Atlantic.
    - 5.2 Direct conflicts.
    - 5.3 Competition.
6. Effects of pollution and industrial development.
    - 6.1 New information on pollution.
    - 6.2 New information on industrial development.
7. Other business.
8. Recommendations to the Scientific Committee.
9. Compilation of references for report.
10. Adjournment.

Appendix 2

LIST OF DOCUMENTS SUBMITTED TO THE SMALL CETACEANS SUB-COMMITTEE

SC/33/SM

1 SMITH, T. Changes in size of three dolphin populations (*Stenella spp*) in the eastern tropical Pacific. [Withdrawn.]

2* OGNETOV, G. N. and POTELOV, V. A. The peculiarities of the white whale, *Delphinapterus leucas*, distribution and population dynamics in the White Sea.

3* ALLEN, R. and GOLDSMITH, M. D. Dolphin mortality in the eastern tropical Pacific incidental to purse seining for yellowfin tuna, 1980.

4* EASTON, D., KLINOWSKA, M. and SHELDRICK, M. C. A preliminary analysis of the British strandings records of the Harbour porpoise (*Phocoena phocoena*).

5 ABBOTT, R. M., KLINOWSKA, M. and EVANS, P. G. H. Analysis of the sightings records of the harbour porpoise (*Phocoena phocoena*) in British waters. [Withdrawn.]

6* PERRIN, W. F. and OLIVER, C. W. Time/area distribution and composition of the incidental kill of dolphins and small whales in the U.S. purse-seine fishery for tuna in the eastern tropical Pacific.

7* BRODIE, P. F. Growth and age determination of the beluga *Delphinapterus leucas* based on a captive specimen.

8 Anonymous. Canadian research and management proposals related to narwhal and beluga, 1981.

9 FINLEY, K. J., MILLER, G. W., ALLARD, H., DAVIS, R. A., and EVANS, C. R. The white whales (*Delphinapterus leucas*) of northern Quebec: distribution, abundance, stock, identity and catch history.

10* FINLEY, K. J. and MILLER, G. W. The 1979 hunt for narwhals (*Monodon monoceros*) and an examination of harpoon gun technology near Pond Inlet, Northern Baffin Island.

11* DUGUY, R. and HUSSENOT, E. Occasional captures of delphinids in the N.E. Atlantic.

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* Published in this volume.

Appendix 3

REPORTED OR PUBLISHED ESTIMATED CATCHES OF SMALL CETACEANS IN 1981 BY SPECIES AND COUNTRIES

				Denmark					(ETP)						
cies		Canada	Japan	Greenland	Faroes	Norway	USSR	South Africa	USA	Non-USA	Spain	France	New Zealand	Seychelles	Total
rd's beaked whale	D	—	31	—	—	—	—	—	—	—	—	—	—	—	31
rwhal	D	350	—	350[1,2]	—	—	—	—	—	—	—	—	—	—	700
ite whale	D	768	—	550[1,2]	—	—	236	—	—	—	—	—	—	—	1,554
lo.-Pac. hump-backed dolphin	I	—	—	—	—	—	—	8	—	—	—	—	—	—	8
se killer whale	D	—	356[1]	—	—	—	—	—	—	—	—	—	—	—	356
	I	—	21[1]	—	—	—	—	—	—	—	—	—	—	—	21
ler whale	D	—	2	—	—	52	—	—	—	—	—	—	—	—	54
ng-finned pilot whale	D	—	—	2[1,2]	2,773	—	—	—	—	—	—	—	—	—	2,775
	I	3	—	—	—	—	—	—	—	—	—	—	—	—	3
ort-finned pilot whale	D	—	686[1]	—	—	—	—	—	—	—	—	—	—	—	686
	I	—	6[1]	—	—	—	—	—	—	—	—	—	—	—	6
sky dolphin	I	—	—	—	—	—	—	—	—	—	—	—	—[4]	—	—[4]
	L	—	—	—	—	—	—	1	—	—	—	—	—	—	2
cific white-sided dolphin	D	—	69[1]	—	—	—	—	—	—	—	—	—	—	—	69
	I	—	4[1]	—	—	—	—	—	—	—	—	—	—	—	4
ttlenose dolphin	D	—	3,480[1]	—	—	—	—	13	—	—	—	—	—	—[5]	3,493
	I	—	13[1]	—	—	—	—	—	—	—	5	3	—	—	21
sso's dolphin	I	—	3[1]	—	—	—	—	—	—	—	—	1	—	—	4
antropical] spotted dolphin	D	—	1,440[1]	—	—	—	—	—	—	—	—	—	—	—	1,440
	I	—	20[1]	—	—	—	—	—	10,932[2]	11,637[2]	—	—	—	—	22,589
inner dolphin	I	—	—	—	—	—	—	—	4,334[2]	10,884[2]	—	—	—	—	15,218
iped dolphin	D	—	16,247[1]	—	—	—	—	—	—	—	—	—	—	—	16,247
	I	—	97[1]	—	—	—	—	—	75[2]	342[2]	—	4	—	—	518
mmon dolphin	D	—	49[1]	—	—	—	—	—	—	—	—	—	—	—	49
	I	—	75[1]	—	—	—	—	89	400[2]	4,621[2]	—	7	5[4]	—	5,197
arbour porpoise	D	—	30[1]	850[1,2]	—	—	—	—	—	—	—	—	—	—	880
	I	—	10[1]	—	—	—	—	—	—	—	—	1	—	—	11
all's porpoise	D	—	6,718[1]	—	—	—	—	—	—	—	—	—	—	—	6,718
	I	—	9,158[7]	—	—	—	—	—	—	—	—	—	—	—	9,158
nless porpoise	D	—	153[1]	—	—	—	—	—	—	—	—	—	—	—	153
eaviside's dolphin	I	—	—	—	—	—	—	1	—	—	—	—	—	—	1
ector's dolphin	I	—	—	—	—	—	—	—	—	—	—	—	1[4]	—	1
nidentified or mixed	I	23,399[6]	9[1]	6[1]	—	—	—	61	314[2]	—	—	—	150[1,2,4]	≤100	24,039
otal		24,520	38,677	1,758	2,773	52	236	174	16,055	27,484	5	16	156	≤100	112,006

Legend: D = Direct
I = Incidental
L = Live capture

1 = Provisional.

2 = Estimated total.

3 = Non-USA kill in ETP.

4 = 1980/81—Catch listed under 'other' composed of dusky, common, and Hector's dolphins, unspecified proportions.

5 = Most of the estimated ≤100 reported are bottlenose dolphins.

6 = Actual takes of 254 animals, of mixed-species composition with unreported proportions, extrapolated to numbers of nets fishing off Newfoundland (SC/33/PS13). As noted in the text, the estimate is of questionable value, because data from a small sample of fishermen (100) in one area were extrapolated to the entire Newfoundland coast and because most of the fishermen queried reported no take (nearly all of the 254 reported were taken by a few fishermen in one location).

7 = Estimated by US (SC/33/ProgRep USA).

Appendix 4

ABUNDANCE ESTIMATES FOR KILLER WHALES IN THE ANTARCTIC

P. S. Hammond

Ohsumi (SC/Jn81/KW10) has calculated population estimates of killer whales in areas I–VI of the Antarctic. He used indices of abundance from Japanese scouting boat data collected from 1965–1980 calibrated to a population estimate made by Allen (*Rep. int. Whal. Commn* 31: 151–152) who employed line-transect methodology on data collected during the IWC/IDCR minke whale cruises in 1978/79 and 1979/80. The calibration involved calculating the ratio of the IDCR population estimate to the scouting boat index of abundance for data collected in Areas III and IV, zone B, in January in both cases. Population estimates for all areas were then calculated by multiplying the indices of abundance from the scouting boat data by this ratio.

One of the assumptions of this method is that the survey areas for the two data sets upon which the ratio depends are equal. This was not the case. The scouting boat index of abundance was calculated assuming a survey area of 1,560,000 sq. nm and the IDCR population estimate was calculated assuming a survey area of 960,500 sq. nm.

The sighting rates (number of whales seen/length of search track in nm) from the two data sets turn out to be very similar in the calibration area; 0.030 for the scouting boat data and 0.028 for the IDCR data. This indicates that given similar sighting conditions the two surveys were sampling the same population density. If it is assumed that sighting conditions were the same, an estimate of density of whales from the scouting boat sighting rate can be obtained by multiplying by the factor which converts sighting rate to density using the IDCR data. The number of whales in the area surveyed by the scouting boats can then be obtained by multiplying scouting boat density by the survey area. Since sighting rate can be obtained for the scouting boat data by dividing the index of abundance by the survey area, and the population estimate is obtained by multiplying by the survey area, the only calculation necessary to get from the scouting boat index of abundance to a population estimate is to multiply by the sighting rate: density estimate conversion factor from the IDCR data. This is given by

$$\frac{\text{Density of whales from IDCR cruises}}{\text{Sighting rate of whales from IDCR cruises}} = \frac{0.0637}{0.0278} = 2.29$$

This conversion factor can then be applied to the indices of abundance for Areas I–VI given in Table 4 in SC/Jn81/KW10 to produce revised population estimates. These are given at the foot of the page.

For these population estimates to be viewed as absolute numbers of whales, several assumptions need to be made: firstly, that the population estimate made by Allen is correct: secondly, that sighting conditions were the same for all surveys in all areas: thirdly, that any non-random searching with respect to killer whale density has been accounted for by the stratification schemes.

There is clear evidence that the density of minke whales in the Antarctic decreases very sharply from the ice edge to the north within 5° of the ice edge (*Rep. int. Whal. Commn* 30: 257–283; SC/Jn81/MiS15; SC/Jn81/MiS16). If killer whales are distributed similarly to minke whales, killer whale density will not be homogeneous within the 5° squares next to the ice edge. If searching effort has been directed towards regions of high minke whale density, estimates of sighting rates and densities of killer whales may be biased upwards.

Prior to 1970, the primary target of the Japanese scouting boats was the sei whale. Since 1970, the primary target has been the minke whale.

	Area						
	I	II	III	IV	V	VI	Total
Index of Abundance	11,565	17,082	37,290	30,921	6,953	7,503	111,314
Population estimate	26,500	39,141	85,445	70,851	15,932	17,192	255,061

Annex I

Meeting Procedures (see Agenda Item 4.1)

Item 26.2(d) of the Commission's 32nd Meeting Report (*Rep. int. Whal. Commn* 31: 27) endorses the Finance and Administration Committee's recommendation that:

> 'The Scientific Committee consider methods of reducing its work load, including, for example, a critical examination of only one third of the whale stocks each year with an overview of all stocks to ensure detection of unexpected changes in population estimate.'

The Committee believes that the framework for handling the problem of its excessive workload already exists, given the present system of sub-committees and special meetings. In addition the relatively small number of stocks currently exploited already results in a fairly high proportion of stocks only being 'overviewed' each year.

Given the above, however, the Committee recognises the need for clarification of the priorites to be given to particular stocks in its programme of work each year. It believes that priorities should be assigned as follows:

Priority 1. Those stocks exploited currently as primary targets of a fishery:
Detailed examination, and where necessary, assessment, should be conducted at least every other year;

Priority 2. All other exploited, or currently protected stocks:
Detailed examination should be undertaken every three to four years.

Additional points are:

(i) As a general rule major new assessments should not be undertaken during annual meetings, although 'reruns' may be possible using validated models, or revised parameter values, or new data sets, particularly where these have been developed by national groups between meetings and are available in checked form on the IWC system at the start of the meeting. Major reassessments involving validation of new models and/or refinement of new data sets should be reserved for Special Meetings or Workshops, although validation itself could be undertaken at annual meetings.

(ii) Major runs of programs not already 'up and running' on the computer, or that require major manipulation of data banks, should not be considered during the annual meeting.

(iii) During the annual meeting, sub-committees should identify priority stocks, and priorities for work to be done in relation to them during the following year. Such work should include assessments, using established programs and data banks, by the IWC computer centre as well as the accession of major quantities of data into the data bank.

RECOMMENDATION

In response to the Commission's request contained in their 26.2(d) of the 32nd Meeting Report the Committee recommends endorsement of the above by the Commission.

Annex J

Whale Marking—Progress Report 1981

S. G. Brown

Information on the progress of whale marking is available in the following Progress Reports: Denmark, Iceland, Japan, New Zealand, Norway, Peru, South Africa, USA, USSR. Recent marking is also referred to in SC/Jn81/KW1 SC/33/Ba6; Mi1, Mi5; PS1 and SC/Jn81/MiS10, 19, 21, 23, 28, 31 and 33. SC/Jn81/MiS19 is a report on the third IDCR Minke Whale Assessment Cruise 1980/81.

At the June 1980 meeting of the Scientific Committee, six proposed marking programmes were approved (*Rep. int. Whal. Commn* 31: 155) for the Antarctic season 1980/81 and for 1981. Marks and marking guns as required were to be supplied by the International Marking Scheme. The IDCR Minke Whale Assessment Programme and the Bryde's whale marking in the South Pacific were carried out in the 1980/81 season.

Details of the numbers of whales marked in the 1980/81 season programme and of marking in 1980 and early 1981, are given in Table 1. The total of 753 large whales marked in the Southern Hemisphere comprises 1 blue, 5 sei, 20 Bryde's, 608 minke and 119 sperm whales.

In the North Atlantic 57 whales were marked in 1980; 18 fin, 33 sei, 4 humpback, 1 minke and 1 sperm whale. In the North Pacific 194 whales were marked in 1980; 2 blue, 1 fin, 3 sei, 55 Bryde's, 29 bowhead, 88 gray and 16 sperm whales.

In addition to the above large whales, 6 killer whales were marked in the North Atlantic in 1980 and 1981 by Norway, and 2 killer whales in 1980 by Iceland. A single killer whale was marked in the North Pacific (Bering Sea) by USSR in 1980.

A fin whale was successfully tagged with a radio tag on the Icelandic whaling grounds in 1980 and tracked for approximately 1,500 km across Denmark Strait to the coast of East Greenland. The USA is conducting experiments in radio tagging bowhead whales, and is developing a tag for use with a Nimbus satellite in tracking dolphin movements. A technique for 'freeze-branding' bottlenose dolphins has also been developed.

One Southern right whale was marked with an experimental streamer mark of New Zealand design off the Auckland Islands in November 1980.

Recoveries of marks in 1980 are reported from 3 fin, 1 sei and 4 minke whales in the North Atlantic and 2 Bryde's whales in the North Pacific. In the Southern Hemisphere marks were returned from 13 minke whales in the 1980/81 whaling season, and from 1 Bryde's whale off Peru in 1981.

Proposed Marking Programmes

Marking programmes proposed for 1981/82 and 1982, including continuing programmes from earlier seasons are listed in Table 2, with estimated requirements of marks, guns, and estimated costs at current and 1982 prices of marks. Rough estimates of shipping costs are included.

Table 1

Large whales marked with Discovery-type marks during 1980 and 1981, and in the Antarctic Season 1980/81

	Blue	Fin	Sei	Bryde's	Humpback	Minke	Bowhead	Gray	Sperm	Total
Southern Hemisphere										
IDCR Minke Whale Cruise 1980/81	—	—	—	—	—	474	—	—	12	486
Japan (Scouting Boat 1980/81)	—	—	5	20	—	134	—	—	91	250
USSR Scheme 1980/81	1	—	—	—	—	—	—	—	8	9
Peru (March 1981)	—	—	—	—	—	—	—	—	8	8
Total	1	—	5	20	—	608	—	—	119	753
Northern Hemisphere—North Atlantic										
Denmark – Norway Joint Cruise 1980	—	8	—	—	4	1	—	—	—	13
Iceland 1980	—	10	33	—	—	—	—	—	1	44
Total	—	18	33	—	4	1	—	—	1	57
Northern Hemisphere—North Pacific										
Japan 1980	2	1	3	55	—	—	—	—	16	77
USSR 1980	—	—	—	—	—	—	29	88	—	117
Total	2	1	3	55	—	—	29	88	16	194

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SC/33/Rep4

Report of the Workshop on Identity, Structure and Vital Rates of Killer Whale Populations, Cambridge, England, June 23–25, 1981

1. PARTICIPANTS AND AGENDA

Members (M) of the Scientific Committee of the IWC, invited experts (E) and observers (O) attending were G. Anderson (M), K. Balcomb (E), P. Best (M), M. Bigg (E), R. Borodin (M), H. Braham (M), I. Christensen (M), M. Dahlheim (E), W. Evans (E), L. Fleischer (M), J. Ford (E), M. Ivashin (M), S. Leatherwood (E), C. Lockyer (M), S. Ohsumi (M), T. Øritsland (M), W. Perrin (M), Y. Riazantsev (M), T. Smith (M), P. Spong (O) and R. Walker (E). Some participants did not attend all sessions of the meeting.

Perrin chaired the meeting and edited the report. Bigg, Dahlheim, Ford and Balcomb acted as rapporteurs.

The draft Agenda was discussed and approved with some additions (Appendix 1). The scope of the meeting was broadened to include consideration of vital rates.

2. BACKGROUND OF THE MEETING

During attempts at the 1980 meeting of the IWC Scientific Committee to assess the status of recently exploited stocks of killer whales, it became apparent that information available to the meeting was not adequate to allow delineation of management units with confidence. For this reason it was decided to convene a meeting of experts on killer whales for the purposes of reviewing all relevant information and making recommendations for definition of management units. A brief review of recent developments in the major killer whale fisheries follows.

2.1 The Northeastern Atlantic

After a 5-year period of very low catches (0–7 per year), in 1978 Norway took 63 killer whales under a license-subsidy system occasioned by the belief that concentrations of killer whales in certain fjord areas were doing harm to depleted but recovering herring stocks. The 1979 take was 221. The killer whales were taken by 'small-type whaling' vessels that usually take minke whales. The catches were processed for oil and animal food. As no stock assessment had been made, the Scientific Committee recommended in 1979 that Norway be urged to provisionally limit its take in 1980 to 52 whales (the average annual coastal take over the 10-year period 1969–78) and be requested to produce at the 1980 meeting the information necessary for an assessment. The recommendation was not acted on by the Commission, but Norway voluntarily limited its take in 1980 to 52 whales, all taken in January. No data on abundance and stock structure were made available at the 1980 meeting, however, and the Committee recommended that the stock(s) be classified provisionally as Sustained Management Stock(s) (on the grounds that there has been a long history of sustained catches), that the catch be limited to 52 whales, and, again, that Norway be asked to conduct research that would make possible a stock assessment. The Committee was especially concerned that the historical catches may not have been all from the same population(s) presently being fished.

2.2 The Southern Hemisphere

Pelagic catches of killer whales by the USSR in the Southern Hemisphere in the 1950s were as high as 110 per season (1958/59 season), but from the mid-1960s until recently they ranged from 0 to 48 per season. Takes of 78 whales were reported in the 1977/78 season and 49 in the 1978/79 season. In 1979 the Committee recommended that the USSR be requested to provide at the 1980 meeting the information necessary for a stock assessment and that the take during the 1979/80 season be provisionally limited to 24 whales, the average season's take over the period 1969–78. The Commission did not act on the recommendation, and the USSR took 916 killer whales during the 1979/80 season. The USSR did not provide information at the 1980 meeting adequate for a stock assessment, but abundance estimates for portions of the Southern Hemisphere (Statistical Areas III and IV) were made based on sightings data from IDCR minke whale cruises in 1978/79 and 1979/80. Data and hypotheses suggestive of the existence of several stocks of killer whales in the Southern Hemisphere were available, but it was felt that there was insufficient evidence on which to base geographical stock boundaries which would be of long-term use for assessments. Because of the uncertainty over stock identities and a lack of knowledge about population parameters and the effects of exploitation on social structure, the Committee recommended that the catch limit for Antarctic killer whales be set at zero. The Commission adopted this recommendation and broadened the existing moratorium on factory-ship whaling (for other than minke whales) to include killer whales.

3. REVIEW OF EXISTING INFORMATION

3.1 Distribution and Migration

3.1.1. North Atlantic

Killer whales in the North Atlantic occur with varying density in different areas. They are frequently observed off Greenland, Iceland, in the Barents and White Seas, and off Novaya Zemlya. Norwegian data indicate that killer whales occur in coastal waters all year round and that there are concentrations in the Lofoten, Møre, and Finnmark areas (SC/Jn81/KW1). Little is known about killer whale movements there, although it was suggested that they migrate in response to movements of their prey. Killer whales are also reported off Great Britian, Iceland, Denmark and France.

In the northwest Atlantic, killer whales remain in the cold waters of the Arctic until driven out by ice. Sergeant and Fisher (1957) reported killer whales off the eastern

Canadian coast (Baffin Island and Lancaster Sound), noting that their appearance in the area may be related to the movements of rorquals and seals. Areas of concentration were noted in the Straits of Belle Island, off Newfoundland and in the Bay of Fundy. Killer whales have been recorded off the northeastern coast of the USA, with a marked decline in numbers of observations to the south (Fig. 1).

A review of the North Atlantic distribution suggests a preference for coastal and continental-shelf waters.

3.1.2. Southern Hemisphere

Data from the Southern Hemisphere suggest that the killer whale is widely distributed, occurring in off-shore as well as coastal areas (SC/Jn81/KW10; Mikhalev *et al.*, 1981) (Fig. 2).

Areas of concentration are apparent in the waters near Antarctica (SC/Jn81/KW10 and SC/Jn81/KW5), off Tasmania, New Zealand and along the western coast of South America. A corridor of high density has been observed between the tip of South America and the Antarctic Peninsula (SC/Jn81/KW5; Brownell, 1974). Killer whales are regularly seen near South Georgia and the South Orkney Islands, thence southward to the Antarctic ice edge (SC/Jn81/KW5). Observations have been made off Cape Town, South Africa, but sightings decrease northward along both coasts of Africa (Dahlheim, 1981). Killer whales are occasionally seen in lower latitude areas of the Indian Ocean (Best, 1971). A north/south migration was proposed (SC/Jn81/KW10; Mikhalev *et al.*, 1981) from low latitudes in the spring to high latitude waters in summer, with a return to low latitudes in autumn (March).

These data are preliminary, and it was suggested in the meeting that they be re-examined in relation to effort. It was pointed out that while no sightings are reported for high latitudes during the austral winter, there has been no sighting effort there at that time. Minke whales migrate north in the fall, but large numbers of seals and penguins (killer whale prey) overwinter in high latitudes. The group concluded that at least part of the picture indicating migration of killer whales north in the fall could well be artifactual.

Killer whales occur off New Zealand and Tasmania during the austral summer. The data suggest that some animals may remain in the lower latitudinal waters and not undertake an extensive migration to the Antarctic region.

3.1.3 North Pacific

Killer whales occur throughout the Bering Sea and have been reported as far north as the Chukchi and Beaufort Seas (Tomilin, 1957) (SC/Jn81/KW2) and as far east as the eastern Beaufort Sea (Richardson (ed.), 1981). Sightings are concentrated near the 200 m contour over the shelf slope in the southeastern Bering Sea; in Unimak Pass and near the Aleutian Island chain; in the waters off Kodiak Island; in Prince William Sound and off southeastern Alaska (SC/Jn81/KW2). These data indicate preference for continental shelf waters. Little is known about killer whale movements within these areas. In the Beaufort, Chukchi and northern Bering Seas they undoubtedly move south with the advancing pack ice and thus long-range movements must occur. Local, more restricted movements may occur in other areas of Alaska. Year-round occurrence of killer whales is documented in the waters of southwestern, southern and southeastern Alaska. Year-round and seasonal occurrence of killer whales are recorded for the inland waterways of British Columbia and Washington State (SC/Jn81/KW4 and SC/Jn81/KW9). Some pods in this area are known to range approximately 370 nm (SC/Jn81/KW2).

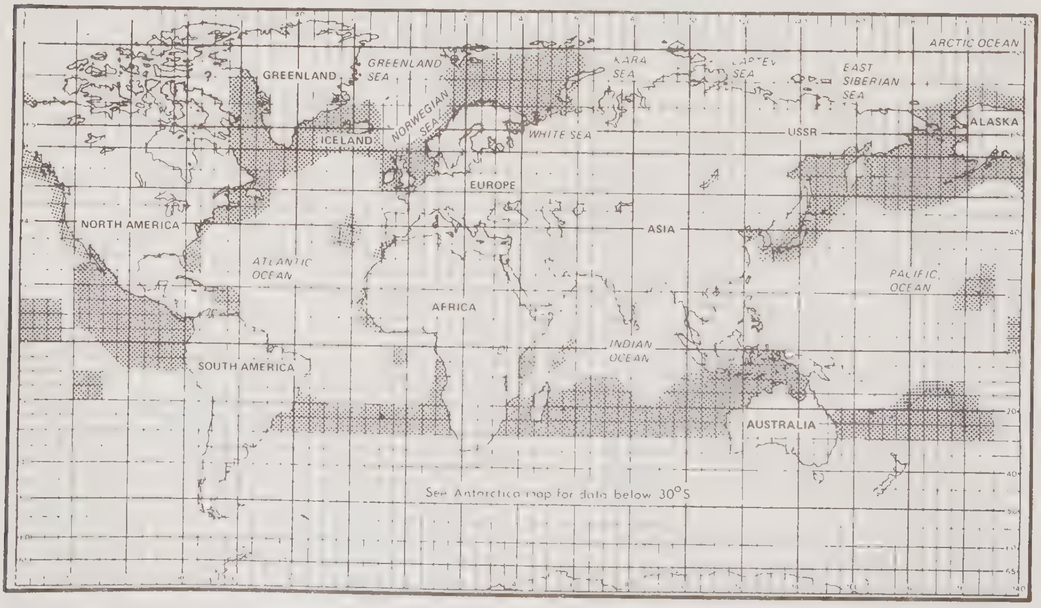

Fig. 1. Distribution of killer whales, *Orcinus orca*, north of 30°S latitude from available published sightings (see Appendix 3 for references used by area).

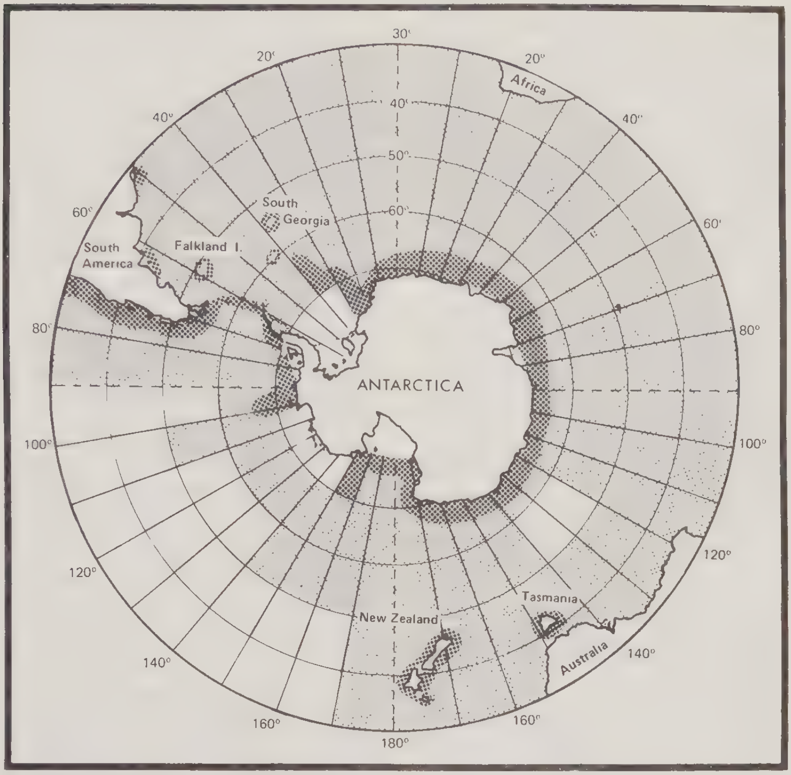

Fig. 2. Distribution and areas of seasonal concentration (dark shading) of killer whales south of 30°S latitude from published sightings (references in Appendix 3).

Sporadic occurrence is noted for the coasts of Washington, Oregon and California (Dahlheim, 1981). In the warm-temperate and tropical Pacific, records of killer whales extend along the Pacific coast from 35°N to just below 5°S (SC/Jn81/KW3). The majority of these records are within 600 km of the mainland coast. Sporadic sightings also occurred in the Gulf of California. Two clusters of observations occurred (1) from 7° to 14°N, 127° to 139°W, and (2) within a band between the equator and 5°N from the Galapagos Islands to 115°W. No seasonal pattern was apparent which could not be readily related to variable effort.

In the western North Pacific, killer whales occur frequently along the Soviet coast in the Bering Sea, in the Sea of Okhotsk, off the eastern side of the Kurile Islands, and off Japan and China (Tomilin, 1957; Nishiwaki and Handa, 1958; Wang, 1979). Here also, a preference for coastal waters is suggested. Little is known about movements in the northwest Pacific. Occasional sightings have also been made in the mid-Pacific (Fig. 1).

3.2 Geographical variation

3.2.1. Morphology

3.2.1.1. External and skeletal size and shape

Mikhalev *et al.* (1981) presented data on external size and shape indicating existence of a 'dwarf' form of the killer whale in the Southern Hemisphere (discussed below under 'Species identity'). The group reviewed the available data and agreed that bimodality in several character suites supports the idea that more than one breeding population exists in the Southern Hemisphere. The dwarf form was first recognised to exist in the course of analyses of data and specimens from the Amundsen Gulf (Appendix Fig. 1 in Mikhalev *et al.*, 1981), but what is not clear from the information available to the meeting is the procedure by which specimens from other areas (Brazil, the Antarctic Peninsula, the South Atlantic off Argentina and other areas) were assigned to the dwarf form. Ivashin agreed to investigate the matter and bring information on the procedure to next year's meeting of the IWC Scientific Committee.

Evans (SC/Jn81/KW11) reported that studies underway by Berzin and Vladimirov at TINRO may result in the description of a morphologically distinct form of killer whale that inhabits the ice edge and ice leads of the Antarctic. Details of this work are not yet available.

Length-frequency data from unaged animals (Table 1, *Rep. int. Whal. Commn* 31: 143) indicate a three to four foot (91–122 cm) difference between median lengths from Norway and those from the Antarctic, with the Norwegian animals being on the average smaller. Mikhalev *et al.* (1981) compared length data for 4 sub-areas of the Antarctic. For males, they found statistically significant differences between the samples from Area I, which contains most of the 'dwarf' animals, and those from the other three Areas, but found no differences among Areas 2, 3 and 4. For females, they found significant differences between Area 1 and Areas 2 and 4, and between Areas 1 and 2. They pointed out, however, that the samples had not been stratified by age. Also, Ivashin cautioned that some selectivity for large animals may exist in the fisheries. The same caution applies to the Norwegian data.

No useful analyses of geographical skeletal variation exist, but Braham reported that series of osteological specimens that would possibly allow such analysis exist at the US National Marine Mammal Laboratory, Seattle and elsewhere. The group agreed that a first step in this direction should be to compile a list of available materials.

3.2.1.2. Meristics

As is the case with skeletal variation, no useful analyses of geographical variation in meristic characters exist, but accumulating material may now make possible analyses such as those carried out by Soviet scientists (Yablokov, Berzin and others) on phalangeal counts in *Delphinapterus leucas* and *Physeter macrocephalus*. Evans reported (pers. comm. from A. Yablokov) that data collected in the Antarctic during the 1979/80 season included toothcounts.

3.2.1.3. Colouration

The group discussed the work of Yablokov and Evans (SC/Jn81/KW11) on variation in colour pattern. Statistically significant geographical variation was found in four of fourteen catalogued *Orcinus* colour-pattern components. Antarctic specimens have a distinct dorsal cape; those from the Northern Hemisphere, South Pacific and South Atlantic lack such a cape. Differences in shape and position of post-ocular patches were observed between specimens from McMurdo Sound – Ross Sea – Antarctic Peninsula and specimens from IWC Areas III, IV and V. These colour-pattern differences support the conclusion that regional groups exist in the Antarctic. However, for some areas the samples represent as few as 5–20 individuals, possibly drawn from single pods (SC/Jn81/KW11).

Detailed examination of colouration of 110 males and 106 females taken by the Soviet whaling fleet in 1977–78, 78–79 and 79–80 further distinguishes animals collected in Area I from those taken in III and IV combined and suggests existence of separate 'in-ice' and 'open water' forms. No significant sexual dimorphism in colouration was found in this sample.

The results of these analyses are consistent with the existence of at least two forms in Antarctic waters but are inconclusive with respect to the 6–8 longitudinally-defined stock divisions proposed by Mikhalev *et al.* (1981).

In British Columbia there are distinct differences in colouration between pods (SC/Jn81/KW4 and KW9). The apparent differences between 'in-ice' and 'open water' forms noted for the Antarctic may be sufficient to mask such pod or area differences there (Table 4 SC/Jn81/KW11). Therefore, there is concern that photographic sample sizes must be substantially increased to ensure that pod-level differences are not misinterpreted as population-level differences or vice-versa.

3.2.2. Sound production

Reports submitted to the meeting describe variation in the vocal patterns of killer whales related to pod and population identity and geographical location. A study of the acoustic behaviour of killer whales in British Columbia (SC/Jn81/KW8) has shown that the predominant social signals are repetitious, pulsed calls which can be organised into discrete, non-overlapping categories. Repeated encounters with 15 photographically-identified pods in this region during 1978–80 demonstrated that each pod has a limited repertoire of 8 to 15 ($\bar{x} = 11.9$) discrete call types. These repertoires are consistent regardless of changes in behavioural context. Recordings obtained from captive animals of known pod origin indicate that pod repertoires are highly stable for periods of at least 15 years (1965–80), and that each pod member produces most or all of the group's calls.

Significant differences exist between the discrete-call repertoires of different pods in British Columbia. Individual pods can be reliably identified solely on the basis of dialectal variation. The degree of similarity in dialects is also a reliable index of the degree of association of pods. Pods which associate and travel together (a pod 'community') tend to share certain calls in their repertoires, while those that do not associate (different communities) produce entirely different calls. Pods which associate most often within a community have the greatest dialectal similarity.

Two of the three pod communities off Vancouver Island, B.C., have separate, well-defined ranges, while the third is widely distributed on the coast and occurs within the other community ranges. Since each pod community is acoustically unique, major dialectal differences in this case exist in both geographically separated and socially isolated (but sympatric) communities.

Variation in killer whale vocalisation is also apparent on a larger geographical scale. Studies on the sounds of Antarctic killer whales have noted differences in the frequency structure, timing, and pattern of calls from those recorded in the North Atlantic (SC/Jn81/KW5) and North Pacific (SC/Jn81/KW6 and SC/Jn81/KW7). Vocalisations recorded in the Ross Island area of the Antarctic were reported to be similar in 1980 and 1981 (SC/Jn81/KW6).

It is apparent from these studies that the examination of killer whale sounds represents a potentially important technique for identifying populations and determining their social organisation. The degree of difference in dialects may correlate with the degree of breeding isolation. If so, the pod will be even more useful in identifying populations. While acoustical studies in other areas have identified geographical variation between widely separated regions (SC/Jn81/KW5, KW6, KW7), it is likely that dialectal variation on a local scale also exists within these regions, and the caution stated above with respect to interpretation of colour-pattern data applies here.

3.2.3. Behaviour

There is no evidence of significant geographical variation in the basic behaviour patterns of killer whales, with the exception of that in sound production (Section 5.2.2) and feeding habits, which probably reflect availability of prey (Section 5.2.5). Group sizes and composition are similar in the North Pacific (SC/Jn81/KW2, KW3, KW4, KW9: Dahlheim, 1981), the Bering Sea (Ivashin and Votrogov, 1981), the coast of Norway (SC/Jn81/KW1), the South Atlantic (Budylenko, 1981), and the Antarctic (Budylenko, 1981; Mikhalev *et al.*, 1981). These sources generally report groups of 1 to 100 individuals, with the majority containing between 5 and 20 individuals. In the coastal waters of Washington and British Columbia, groups with less than 20 animals typically represent primary social units, or pods, with stable membership

(SC/Jn81/KW4, KW9; Section 5.5). Stable groups have also been documented in other areas of the world (SC/Jn81/KW9).

There are several reports of large aggregations containing 100 or more killer whales, primarily in the Antarctic (SC/Jn81/KW7; Budylenko, 1981; Doroshenko, 1978), Alaskan (SC/Jn81/KW2) and Norwegian waters (Christensen, 1978), all high-latitude areas. These large groups probably result from the temporary joining of a number of pods and may be related to seasonal peaks in prey density in certain areas. Killer whales in the Antarctic are frequently observed in the company of other cetaceans (Mikhalev *et al.*, 1981), but this may reflect the fact that the sightings have been made from whaling vessels. However, the participants reported that such associations also occur in several other areas.

Opportunistic feeding behaviour associated with human activities is known to have developed in killer whales in various localities. Among these is the unusual relationship between killer whales and shore-based whalers at Eden, Australia during the later 1800s and early 1900s (reviewed by Mitchell and Baker, 1980), a recently developed interaction between killer whales and a drop-line fishery off Tasmania (*Rep. int. Whal. Commn* 31: 147) and similar interactions with a long-line fishery near Iceland (SC/Jn81/KW1). Such occurrences appear to be localized phenomena and may, as in the case at Eden, Australia, involve only one or a few pods. That these behaviours do not seem to spread is suggestive of little exchange of animals between local areas.

3.2.4 Biochemical and chromosomal characters

Polymorphism has been described in the C-banded karyotype of the killer whale (Árnason, Lutley and Sandholt, 1980), and studies are presently underway to compare chromosomes of killer whales from different locations (D. Duffield, pers. comm. to Dahlheim, June 1981). There is preliminary chromosomal and biochemical evidence that certain pods may be genetically isolated (Duffield and Cornell, 1979). The group agreed that while this area of research is promising for future studies of stock identification, it has not yet progressed sufficiently far to be of use in the present exercise.

3.2.5. Feeding habits

Food items found in the stomachs of killer whales encompass a wide range of species (Appendix 4). The list presented is incomplete and does not represent a comprehensive review of the literature or a complete listing for any geographic area. Fish prey from stomach contents may be less likely to be identified to species and thus may be under-represented in the table. Composition of diet varies among areas and within areas, both seasonally and between individuals sampled.

The broad range of diet items is reflected in diverse feeding behaviours associated with different prey. These behaviours have been described by the authors listed in the table.

The present data do not suggest systematic geographical variation in feeding habits not related to distribution of prey.

3.3 History of catches with respect to geographical sub-areas

3.3.1 North Atlantic

As noted above, there has been concern that the long history of take of killer whales by Norway may not pertain to a single breeding population. Christensen reported that all killer whales taken in recent years have been taken in Norwegian fjords and coastal inshore waters. Data in Jonsgård [Christensen (1975) and in catch records (*fide* Christensen)] indicate that about 70% of the killer whales taken by Norway since 1938 were taken from Norwegian coastal waters. In recent reports (see, for example, Christensen, Jonsgård and Rørvik, 1981) the statistics indicate that the take has been from a portion of the coastline, centred about Lofoten.

Christensen reported (SC/33/KW1) the existence of several (7–8) areas of concentrations of killer whales along the coast of Norway. The whales are found in these areas in large numbers throughout the year; there is no evidence of seasonal migration. The coastal statistical reporting areas in Christensen *et al.*, 1981, correspond roughly to the reported areas of concentration of killer whales. Considering these facts and the limited ranges and long-term stability of local populations observed in the Northeastern Pacific (the only areas where killer-whale movements have been intensively studied for long periods of time) the group thinks it likely that the Norwegian fishery may be exploiting one or a few local breeding populations.

3.3.2. Southern Hemisphere

Mikhalev *et al.* (1981), presented catch statistics for the Southern Hemisphere for the period 1969/70–1978–79 by 10-degree square. The catches were concentrated in roughly 3 regions: southeast of Africa, southeast of Australia, and southwest of South America. These areas correlate roughly with the Areas 1, 2 and 3 defined in the same paper for purposes of analysis of geographical variation in length (discussed above). The authors concluded that at least two populations are probably involved. These analyses do not include data from the 916 killer whales taken during the 1979/80 season. To date, the 1979/80 catch statistics have been reported only by expedition (SC/33/ProgRep USSR).

3.3.3 Other Areas

No detailed information on distribution of catch by sub-areas is available for other fisheries.

3.4 Age and structure of catches

3.4.1 Live capture for display

Killer whales taken for display (about 100) in Washington, British Columbia and Iceland have been young males and females, with selection against large bulls. Pods were enclosed, one or more individuals were selected and removed, and the remainder were released. No information was available on catches for display off Iceland.

3.4.2. Soviet pelagic catches in the Southern Hemisphere

Two sets of data giving length composition are available—one for the period 1961/62 to 1978/79 (Mikhalev *et al.*, 1981) and the other for 1979/80 (IWS LVXXXI) and are shown in Table 1.

Size composition of the earliest catches indicates that there was selection for larger animals, with more males than females taken, and some selection for large animals may

Table 1

Length-frequency data for Soviet takes of killer whales in the Antarctic

	Length 11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Totals
1961/62–1978/79																					
Males							2	7	10	21	17	14	27	31	33	24	13	5	1		205 males
Females							4	10	11	20	19	26	15	5	2	—	—	—	—		118 females
																					323
1979/80																					
Males			1	1	4	6	6	13	39	32	52	69	72	45	41	24	9	14	21	1	450 males
Females	1	1	3	6	9	25	66	46	60	85	88	56	17	2	1	—	—	—	—	—	466 females
																					916

also have occurred in the later catches. Ivashin and Evans reported that the 1979/80 catch of 916 killer whales may incorporate an open-water form and an ice-edge form of different sizes. The relationship of those forms to the dwarf form proposed by Mikhalev and Ivashin is not clear, but it is apparent that detailed consideration of the data from the 1979/80 catch will require further analysis of its possible components.

There is little information on the way in which the killer whales were taken, i.e., whether an attempt was made to take all members of a pod or only a small number of individuals selected at random. If possible, the information will be obtained and presented to the Scientific Committee next year. It is understood that there are no data available on the age composition of the recent Soviet catches.

3.4.3 Other coastal catches

Nishiwaki and Handa (1958) gave details of coastal Japanese killer whale catches for the period 1948–57, in which 567 animals were taken:

	1948		1949		1950		1951		1952		1953		1954		1955		1956		1957		Totals	
	no.	size	no.	size	no.	size	no.	size	no.	size	no.	size	no.	size	no.	size	no.	size	no.	size	no.	size
♂	12	19.4	19	21.6	11	22.5	40	21.9	33	21.8	39	21.7	66	22.5	43	20.2	22	21.0	35	21.2	320	21.5
♀	15	18.6	24	18.3	7	20.1	27	19.1	21	20.7	26	21.7	43	21.9	34	19.8	16	21.0	34	18.4	247	20.0

It is clear that there was selection for males, with more males than females taken in all years but 1948 and 1949. The mean lengths of males taken are greater than mean lengths of females in years other than 1953 and 1956, when the mean lengths were equal. Total coastal Japanese catches in the period 1948–80 were 1,452 animals. Detailed information was not available for the period 1958–80 for the Japanese coastal fishery. Similarly, no information beyond that presented by Dahlheim (1981) was available for Denmark, Peru, South Africa, USA or the West Indies.

3.5 Definition of breeding unit

3.5.1 Size

In British Colombian waters, at least, the primary social unit (in which calves are reared) is a pod, and the basic breeding unit is demonstrably no larger than a 'community' composed of several pods (SC/Jn81/KW4; SC/Jn81/KW9). The pod sizes range from 1 to 50 whales. Periodically pods join with others to form larger aggregations of up to 80 individuals. Pods around Vancouver Island form three communities whose individuals associate with one another but not with individuals of other communities. One, a resident community off southern Vancouver Island, contains three pods totalling 79 whales that are seen year round. The second, resident off northern Vancouver Island, contains 12 pods with about 136 whales. At least one of these 12 pods is seen year round. A third community is made up of transient whales which range in a loose network around Vancouver Island, incorporating the ranges of the other communities. This group contains 15 pods and 47 individuals, which are seen infrequently. The transient pods differ from resident pods in swimming and feeding behaviour. They also range farther than do the other two communities.

In other regions, aggregations of several hundred are commonly reported, and in one instance a group of 2,500 was noted in Alaska (SC/Jn81/KW2). There was discussion about the difficulty in counting cetaceans in large groups.

3.5.2 Structure

Pods typically contain individuals of mixed ages and sexes (SC/Jn81/KW4; SC/Jn81/KW9; Grieg, 1889). Based on 30 pods containing 260 whales in British Columbia and Washington, the average pod contains 23.0% bulls, 34.1% cows, 38.5% juveniles and 4.4% young of the year. Solitary whales can be male or female. Some small pods (<7 whales) in British Columbia contain no adult males. Such pods can contain calves and thus must breed with males of other pods. At the opposite extreme is a pod of eight whales of which five are bulls.

3.5.3 Stability

Pods are long-term association of the same individuals (SC/Jn81/KW4; SC/Jn81/KW9; Wellings, 1944). Associations within entire pods have been recorded for seven years in British Columbia and Washington. Four individuals in one pod are known to have associated for 13 years. Based on observed annual changes in pod size, these pods increase at an average rate of 2.52%. One suggestion for new pod formation is that it occurs through the gradual splitting of established pods over perhaps several decades. Related sub-pods would gradually spend less time in association with one another. Evidence is now accumulating to indicate that mothers and their accumulated young form subgroups within pods. Such maternal associations may well be the basis on which pods eventually divide. There have been no instances observed of individuals moving out of one pod and into another on a permanent basis, although temporary associations across pods within a community do occur.

3.6 Vital parameters

3.6.1. Age at sexual maturity

Based upon catches of killer whales by Norway reported by Jonsgård and Lyshoel (1970) and Christensen (SC/Jn81/KW1) and by the USSR in 1979/80 (IWS LXXXVI and Table 1), few pregnancies occur among females less than 16 ft long, and a marked increase in pregnancies occurs among females 16 ft long and larger. These data indicate that most first pregnancies occur at about that length. Age at first pregnancy is not directly known. However, based on rates of growth of captive killer whales (SC/Jn81/KW4) it is at least 7 years. Based on growth layers in the teeth of whales taken in the Norwegian fishery (SC/Jn81/KW1, Fig. 9), both sexes attain the length of 16 ft at an age of about 8 years.

Based upon testes weight and the presence of sperm, as well as the onset of dimorphism of the dorsal fin, males reach sexual maturity at about 19 ft (SC/Jn81/KW4). Age at sexual maturity is not directly known, but based on captive whale growth rates (SC/Jn81/KW4), it is at least 10–12 years. Growth layers in the teeth (SC/Jn81/KW1) indicate that this length is attained at about 16 years.

There are no data on changes in the age at sexual maturity with level of exploitation.

3.6.2 Pregnancy rate

Reported pregnancy rates for adult females ≥ 16 ft vary from 14.8% to 42.3% (SC/Jn81/KW4). However, if gestation is more than 12 months, annual pregnancy rates calculated without allowing for foetuses from more than one breeding season will be too high. As shown in Appendix 5, there is definite bimodality in the length frequencies of foetuses from Antarctic catches. Pregnancy rates (including known pregnancies for females of less than 16 ft) recalculated to provide an annual rate corrected for a 15-month gestation period are given in Table 2.

There may be decreased reproductive activity in older females. Data from Antarctic 1979/80 catches indicate a decreasing proportion of pregnant females over 20 ft. There are in addition data on known pods in which adult females are known to have calved at three-year intervals while others have calved much less frequently or not at all in 7–10 years of observation. It appears that there may be social control maintaining relatively low levels of pregnancy.

3.6.3 Birth rates

Studies in British Columbia (SC/Jn81/KW4) and Greater Puget Sound (SC/Jn81/KW9) provide estimates of birth rate for calves which survived to an age of at least six months. Over the same seven-year study period, both studies yielded identical birth-rate information for pods studied in common, but the British Columbia study included more pods and is used here for a best estimate. Table 3 summarizes their data. The birth rate in cropped pods was slightly higher than that for uncropped pods. The estimated population birth rates correspond well with the observed ratio of 7.45% calves-and-juveniles to other ages noted by Best (1980) in Antarctic sighting cruises. Also, they are close to 2.99% ratio of newborn to other ages observed in aerial surveys in the Ross Sea and McMurdo Sound (SC/Jn81/KW6), although some field observations of higher proportions exist, e.g., Christensen (1978) reported a pod of 4–6 animals with one newborn calf and another pod of 15–20 with 5 small calves. However, while it had been considered that the birth rates for adult females were much lower than the pregnancy rates from some whaling records, a re-examination of pregnancy-rate data indicates a much closer correlation of birth and pregnancy rates (Appendix 6). The Committee discussed the discrepancy in rates but could not establish the cause. It could be due to some selection of pregnant whales by whalers, which could happen if females with calves are more difficult to capture, or due to high mortality of calves in the first six months of life.

3.6.4 Natural mortality rate

Natural mortality rates were estimated based on the disappearance of identifiable individuals in pods in the Vancouver Island study (SC/Jn81/KW4). Bulls, cows and juveniles all exhibited low overall rates. These data are presented in Table 3. In each case the cropped pods had a slightly lower rate than the uncropped pods. Further studies are needed to confirm the rates.

3.6.5 Net annual change in pod size

The annual net pod change was determined by following the sizes of individual pods over several years. The data are given in Table 3. The cropped pods have a slightly higher rate than the uncropped pods (SC/Jn81/KW4 and 9).

3.6.6 Length of gestation

The commonly quoted range for duration of gestation is 12–16 months (Nishiwaki and Handa, 1958). The duration is probably more than 12 months. A bimodal peak in foetal lengths occurred during January-March 1979/80 in the Antarctic (Appendix 6), indicating two developmental stages of foetal growth occurring at the same time. Additional data are available from captive animals. The conception time of a female at Marineland of the Pacific was determined to be at about mid-March 1979, based on progesterone levels (Dahlheim, pers. comm. 25 June 1981) and a calf was born prematurely on 1 April 1980, suggesting a gestation close to 15 months.

3.6.7 Length of lactation

There are no direct observations on the duration of lactation in killer whales, although the calf remains in close association with the mother for about a year after birth.

3.7 Species identity

The group discussed the new species, *Orcinus nanus*, proposed by Mikhalev, *et al.* (1981) based on data and specimens collected in the Southern Hemisphere, 1972–79.

Ivashin explained that the description is based on modal

Table 2

Killer whale pregnancy rates from catch data

Source		Length in feet																			Corrected % annual	
		11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28			
Norway	♀					39	48	55	83	72	53	29	28	9	6	4	2	1	1	430		
(Jonsgård & Lyshoel. 1970)	pregnant					1	8	9	12	10	4	4	5	3	2	0	0	0	1	59	51.6[1]	
	% of mature ♀					2.6	16.7	16.4	14.5	13.9	7.5	13.8	17.9	33.3	33.3	—	—	—	1.00	13.72%	12.00%	
Norway (SC/Jn81/KW1)	♀					9	23	37	35	26	23	5	2	1						161		
(i) foetus present	pregnant					1	11	16	15	6	5	1	0	1						56	46.7[2]	
	% of mature ♀					11.1	47.8	43.2	42.9	23.1	27.7	25	0	100						34.87%	28.9%	
(ii) ovarian examination	♀				7	4	3	16	13	8	8	2								61		
	mature ♀				0	2	2	16	13	8	8	2								51		
	pregnant				—	1	1	7	7	2	2	0								20	16.7[2]	
	% of mature ♀					50.0	50.0	43.1	53.9	25.0	25.0	—								39.22%	32.8%	
Antarctic	♀							4	10	11	20	19	26	15	5	3				118		
(Mikhalev *et al.*, 1981)	mature ♀							2	8	7	15	16	21	15	4	3				91	(50% of total)	
	pregnant								4	2	4	2	7	4	1	1				25	12.5	
1961/62 to 1978/79	% of mature ♀								50.0	28.6	26.7	12.5	33.0	26.7	25.0	33.3				27.47%	13.74%	
(IWS LXXXVI)	♀	1	1	3	6	9	25	66	46	60	85	88	56	17	2	2				466		
	estimated mature ♀	—	1	—	4	—	25	66	46	60	85	88	56	17	2	1				448	small	large
	pregnant		1		1		11	14	15	21	35	32	10	3	—	—				143	57	85
	% of mature ♀	100			25.0	44.0	21.2	32.6	33.0	41.2	36.4	17.9	17.7	—	—					31.92%	12.72%	18.97%

[1] Where corrected value = No. pregnant −0.5 × 3/12 (No. pregnant)

[2] Where corrected value = No. pregnant −0.5 × 6/18 (No. pregnant)

Table 3

Rates of birth, natural mortality and net pod change in cropped, uncropped and combined pods off British Columbia and Washington, 1973–81

Parameter	Source	Cropped (%)	Uncropped (%)	Combined (%)
Birth rate				
Adult females[1]	SC/Jn81/KW4	11.64	8.02	10.30
	SC/Jn81/KW9	8.90	—	—
Population[2]	SC/Jn81/KW4	4.56	3.15	3.90
	SC/Jn81/KW9	2.60	—	—
Natural mortality rate				
Bulls	SC/Jn81/KW4	2.50	3.06	2.81
Cows	SC/Jn81/KW4	0.46	1.52	0.70
Juveniles	SC/Jn81/KW4	1.99	4.35	2.30
Total	SC/Jn81/KW9	0.80	—	—
Net pod change	SC/Jn81/KW4	3.01	1.67	2.52
	SC/Jn81/KW9	2.30	—	—

[1] ≥ 16 ft

[2] $= \frac{\text{No. calves}}{\text{No. all other ages}}$

differences between a dwarf form and the ordinary killer whale in external proportions, weight of gonads, length at attainment of sexual maturity and maximum length. The dwarf form on the average has relatively larger anterior measurements, a higher and longer-based dorsal fin placed closer to the head, larger flippers placed closer to the head, larger flukes and a shorter peduncle than does the ordinary killer whale. The weight of the testes in the dwarf form at 6.1–6.5 m is the same as in the ordinary killer whale at 7.1–7.5 m. The ovaries of dwarf females 18–19 ft long weigh the same as those of 25 ft long ordinary females, and dwarf females 5.6–6 m long have the same number of ovarian corpora as do ordinary females 7.5–8 m long. Maximum length for the dwarf form is 7.5 m in males and 6.5 m in females, as opposed to 9.0 m and 7.7 m in the ordinary form. Ivashin emphasised that further data and analyses are desirable to adequately delineate the differences between the two forms and settle the question of whether a new species or sub-species is involved. He suggested that studies of colour-pattern differences and of sound production may be helpful in this regard. Ongoing studies of 1979/80 data and specimens by Berzin of TINRO, Vladivostok may also contribute to description of variation of killer whales in the Antarctic.

The group believes that the data are more suggestive of sub-specific-level differentiation than of existence of an unrecognised species, as the differences are modal rather than absolute. In any case, under the international rules of zoological nomenclature, the name *Orcinus nanus* Mikhalev *et al.* 1981 is at this point a *nomen nudem,* because it is not accompanied by figure, diagnosis and designation of a holotype specimen. These items will presumably be included in the final description of the dwarf form.

4. SUMMARY OF CONCLUSIONS

4.1 Nearly every area of the world's ocean that has been examined contains killer whales, but there are obvious concentrations of abundance, mainly within a few hundred miles of coasts and in high latitudes.

4.2 There is not a strong case for extensive migrations, with the exception of migration with the retreating ice edge in polar areas. This suggests the existence of local populations.

4.3 There is good evidence for a high degree of isolation over a few hundred miles for coastal animals, but the data are inadequate to define larger units. Pelagic animals may have larger ranges. Some members of the group believe that while the existence of broader regional groupings has been proposed, the application of a broader-scale concept of stock areas for management by analogy with species such as sperm and baleen whales is not appropriate for this species.

4.4 The sorts of population units (groups of pods or 'communities') that can be defined with present methods probably contain only tens or hundreds of animals.

4.5 Given the extreme stability of local populations and the low reproductive rates evidenced by the available data, any exploitation can be expected to have long-term impacts on population size and structure.

5. RECOMMENDATIONS FOR RESEARCH

5.1 Noting that a large sample (916) of killer whales was taken in 1979/80 by the USSR and not yet fully reported upon, the meeting recommends that the USSR be asked to provide a report at next year's meeting of the Scientific Committee detailing the specimens and data available, including analysis of sightings per effort. Also, specific questions were raised about hunting strategy of the whalers which may have biased the age structure and size structures of the catch; these should be addressed by the report.

5.2 Noting that the question of number of stock(s) of killer whales in the waters near Antarctica remains unresolved, the meeting recommends that studies be continued on existing data bases concerning colour patterns and morphology of killer whales taken and that acoustic methods of distinguishing pods and populations by their vocalisations be further explored.

5.3 Noting that the social and breeding population structure of Southern Hemisphere killer whales has not been studied and might be different from that of eastern North Pacific killer whales reported here, the meeting recommends that reports be solicited from other researchers in the Southern Hemisphere to ascertain whether differences exist.

5.4 Noting that specimen materials exist in public museums and various institutions that have not been examined and described in the literature and that they potentially could yield valuable data on age and morphological variation, the meeting recommends that these materials be inventoried and that their study be encouraged.

5.5 Noting that inadequate information exists for stock definition of the killer whale population in Norwegian coastal waters, the meeting recommends that research be carried out to provide this and other information necessary for adequate stock assessment. The programme of marking to study movements should continue. The possibility of using natural marks should be investigated. Considering the existence of a live-capture fishery in Icelandic waters, the same recommendation should be made to Iceland.

5.6 Noting that teeth for age determination have not been consistently collected for all killer whales taken commercially or found stranded, the meeting recommends that in the future every effort be made to collect and examine such materials, as well as gonads, stomach contents, morphometric and meristic data, and other biological materials whenever possible.

5.7 Precise data on locality and date of capture for the live-capture fishery in Iceland and elsewhere should be provided to the Scientific Committee.

5.8 Noting that chromosomal and biochemical studies may yield information concerning stock and populations of killer whales, the meeting recommends that such studies be undertaken for all killer whales currently in captivity, and, whenever opportunity exists, to conduct such studies on stranded and harvested whales and whales in the wild.

5.9 Noting that field studies of killer whales in waters around Vancouver Island and in Greater Puget Sound have produced significant new information concerning vital parameters, as well as precise assessments of the local populations, the meeting recommends that such studies be continued, in order to accurately determine: (1) at what age killer whales become adult, (2) age-specific birth and mortality rates, and (3) immigration/emigration rates for the local population, especially as they may correlate with changes in the habitat. It is further recommended that similar studies be encouraged in other areas of the world for comparative purposes.

5.10 Existing data on dates and localities of take of killer whales in Japanese coastal waters should be made available and analysed to elucidate patterns of distribution and abundance in that area.

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Appendix 1

AGENDA

1. Participants and agenda
2. Background of the meeting
   - 2.1. The northeastern Atlantic
   - 2.2. The Southern Hemisphere
3. Review of existing information
   - 3.1. Distribution and migration
     - 3.1.1. North Atlantic
     - 3.1.2. Southern Hemisphere
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       - 3.2.1.1. External and skeletal size and shape
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     - 3.2.2. Sound production
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     - 3.2.4. Biochemical and chromosomal characters
     - 3.2.5. Food habits
   - 3.3 History of catches with respect to geographical sub-areas.
     - 3.3.1. North Atlantic
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   - 3.6. Vital parameters
     - 3.6.1. Age at sexual maturity
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     - 3.6.4. Natural mortality rate
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     - 3.6.6. Length of gestation
     - 3.6.7. Length of lactation
   - 3.7. Species identity
4. Summary of conclusions
5. Recommendations for research
6. Literature cited
7. Other business
   - 7.1 Production of the meeting report
   - 7.2 Publication of the meeting documents

Appendix 2

LIST OF DOCUMENTS SUBMITTED TO THE MEETING

SC/Jn81/KW1*	Christensen, I. Killer whales in Norwegian coastal waters.
SC/Jn81/KW2*	Braham, H., Dahlheim, M. and Consiglieri, L. Killer whales in Alaska from at sea sightings documented in the U.S. Platforms of Opportunity Program.
SC/Jn81/KW3*	Dahlheim, M., Leatherwood, J. S. and Perrin, W. F. Distribution of killer whales in the warm temperate and tropical eastern Pacific.
SC/Jn81/KW4*	Bigg, M. An assessment of killer whale, *Orcinus orca*, stocks off Vancouver Island, British Columbia.
SC/Jn81/KW5	Jehl, J. R., Evans, W. E., Awbrey, F. T. and Dreischman, W. S. Distribution and geographic variation in the killer whale, *Orcinus orca*, populations in the Antarctic and adjacent waters.
SC/Jn81/KW6	Thomas, J. A., Awbrey, F. T., Leatherwood, J. S. Evans, W. E. and Jehl, J. R. Ross Sea killer whale, *Orcinus orca*, distribution, behaviour, colour pattern and vocalizations.
SC/Jn81/KW7*	Awbrey, F. T., Evans, W. E., Thomas, J. A., and Leatherwood, J. S. Comparison of Ross Sea and Pacific northwest killer whale vocalizations.
SC/Jn81/KW8*	Ford, J. K. B. and Fisher, H. O. Killer whale, *Orcinus orca*, dialects as an indicator of stocks in British Columbia.
SC/Jn81/KW9*	Balcomb, K. C. III., Boran, J. R. and Heimlich, S. L. Killer whales in Greater Puget Sound, a population ideally suited for statistical modelling.
SC/Jn81/KW10	Ohsumi, S. Distribution and abundance of killer whales in the Southern Hemisphere.
SC/Jn81/KW11*	Yablokov, A. V. and Evans, W. E. Geographic variation in the color pattern of killer whales (*Orcinus orca*).

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* Published in this volume.

Appendix 3

LITERATURE CITATIONS DOCUMENTING KILLER WHALE SIGHTINGS CORRESPONDING TO GEOGRAPHIC AREAS OF DISTRIBUTION DEPICTED IN TEXT AND FIGURES 1 AND 2

Area	Literature citations
Atlantic Ocean	
Northeast (including Greenland and Barents Seas)	Geptner (1936) and Chapskii (1941) cited in Tomilin (1957); Jonsgård and Lyshoel (1970); Christensen *et al.* (1981); SC/Jn81/KW1.
Northwest	Sergeant and Fisher (1957).
Central	
Caribbean	Caldwell and Caldwell (1975).
Azores	Clark (1981).
West Africa	Bourne (1965) cited in Mitchell (1975); Evans and Yablokov (In ms).
Southern	
South America	Aguayo (1975); Budylenko (1981).
Africa	Budylenko (1981).
Pacific Ocean	
Northeast	
Alaska	Wada (1981); SC/Jn81/KW2.
North America and Mexico	Scheffer and Slipp (1948); Norris and Prescott (1961); Pike and MacAskie (1969); Balcomb *et al.* (1980); SC/Jn81/KW3, SC/Jn81/KW4; SC/Jn81/KW9.
Northwest	
Japan–China	Nishiwaki and Handa (1958), Kasuya [illegible] (1971); Wang (1979); Anon. (1981); Wada (1981).
Pacific Ocean (continued)	
USSR	Zenkovich (1938); Nikulin (1941); Tomilin (1957); Sleptsov (1961); Ivashin and Votrogov (1981).
Central	
Eastern	SC/Jn81/KW3.
Hawaii	Richards (1952) cited in Leatherwood and Dahlheim (1978). SC/Jn81/KW3.
Southern	
South America	SC/Jn81/KW10.
Western	Blokhin (1981); SC/Jn81/KW10.
Indian Ocean	
Africa	Best (1971).
Australia	Blokhin (1981).
Arctic Ocean (US)	Cook (1926); Sleptsov (1961); Richardson (1981).
Antarctic Ocean	
Atlantic	Brownell (1974); Jehl *et al.* (1980); Dahlheim (1981).
Pacific	Brownell (1974); Jehl *et al.* (1980); Dahlheim (1981).
Indian	Brownell (1974); Best (1980).

Appendix 4

FOOD ITEMS OF KILLER WHALES BY GEOGRAPHIC AREAS

Area	Food Items	References
Atlantic Ocean		
Northeast	Herring (*Clupea spp.*) cod and squid, 'seal', birds (Norway), salmon (England).	Lepekhin (1805) cited in Tomilin (1957); Pike and MacAskie (1969); Jonsgård and Lyshoel (1970); Norman and Fraser (1949) cited in Martinez and Klinghammer (1970); SC/Jn81/KW1.
Northwest	Minke whale (*Balaenoptera acutorostrata*), seals (harp seal? *Phoca groenlandica*).	Sergeant and Fisher (1957).
Caribbean (St Vincent)	Leatherback turtle (*Dermochelys coriacea*), pygmy sperm whale (*Kogia breviceps*), *Stenella spp.*, sperm whale (*Physeter macrocephalus*), squid.	Caldwell and Caldwell (1969); R. V. Walker (unpublished).
Southern	Dolphins, fishes, pinnipeds.	Shevchenko (1975) cited in Budylenko (1981).
Pacific Ocean		
Arctic and Sub-Arctic	Walrus (*Odobenus rosmarus*), bearded seal (*Erignathus barbatus*), ringed seal (*Phoca hispida*), salmon (*Oncorhynchus spp.*), northern sea lion (*Eumetopias jubatus*), Alaskan fur seal (*Callorhinus ursinus*), gray whale (*Eschrichtius robustus*), bowhead whale (*Balaena mysticetus*), white whale (*Delphinapterus leucus*).	Scammon (1872); Cook (1926); Zenkovich (1938); Nikulin (1941); Nishiwaki and Handa (1958); Fay *et al.* (1979); SC/Jn81/KW2.
Northeast	California sea lion (*Zalophus californianus*), elephant seal (*Mirounga angustirostris*), Dall's porpoise (*Phocoenoides dalli*), harbor porpoise (*Phocoena phocoena*), striped dolphin (*Stenella coeruleoalba*), salmon, Pacific halibut (*Hippoglossus hippoglossoides*), merganseropah (*Mergus serrator*), harbor seal (*Phoca vitulina*), deer (*Odocoileus sp.*), squid (moon fish), carcharhinid shark, minke whale, blue whale (*Balaenoptera musculus*), ray (*Torpedo californica*), common dolphin (*Delphinus delphis*), greenling (*Hexagrammidae sp.*), Ling cod (*Ophiodon elongatus*).	Scheffer and Slipp (1948); Brown and Norris (1956); Nishiwaki and Handa (1958); Norris and Prescott (1961); Rice (1968); Barr and Barr (1972); Tarpy (1979); Balcomb *et al.* (1980);
Northwest	Cod (*Gadus* spp.), flatfish, sardine, salmon, tuna, mackerel, Atka mackeral, bonito, cephalopods (squid and octopus), Dall's porpoise, striped dolphin, Baird's beaked whale (*Berardius bairdii*), goose-beaked whale (*Ziphius cavirostris*), sei whale (*Balaenoptera borealis*), pilot whale (*Globicephala macrorhynchus*), finless porpoise (*Neophocaena phocaenoides*), harbor seal.	Nishiwaki and Handa (1958).
Southern	No data.	

Appendix 4—*continued*

Area	Food Items	References
Indian Ocean	Pygmy sperm whale (*Kogia* spp.), minke whale (*Balaenoptera acutorostrata*), elephant seal (*M. leonina*).	P. Best (unpublished).
Antarctic	Antarctic cod (*Dissostichus mowsoni*), adelie penguin, crabeater seal (*Lobodon carcinophagus*), minke whale, pinnipeds, squid, fish, leopard seal (*Hydrurga leptonyx*), southern elephant seal (*M. leonina*).	Ivashin (1981); Mikhalev *et al.* (1981); Siniff and Bangston (1977) and Carrick and Ingham (1962) cited in Smith *et al.* (1981); SC/Jn81/KW6.
Other	Skate, smelt, capelin, herring (*Clupea harengus*), right whale (*Balaena glacialis*), humpback (*Megaptera novaeangliae*), fin whale (*Balaenoptera physalus*), narwhal (*Monodon monoceros*), Weddell seal (*Leptonychotes weddelli*), sea otter (*Enhydra lutris*), white winged scoter (*Melanitta fisca leglandi*), black brant (*Branta nigricans*).	Tomilin (1957); Martinez and Klinghammer (1970).

Appendix 5

A RE-EXAMINATION OF PREGNANCY RATES AND CALF RATIOS IN *ORCINUS ORCA*

G. R. V. Anderson

INTRODUCTION

Estimates of pregnancy rates, and hence of expected numbers of young-of-year, observed birth rates and calf ratios have been reported as ranging from 5–42%. Variations of such magnitude may arise from extreme bias in sampling or for other reasons, and some resolution is required. Data from the 1979/80 USSR catch of killer whales in the Antarctic have been re-examined and pregnancy rates and expected numbers of young-of-year recalculated with account taken of a gestation period of 15 months.

PREGNANCY RATE DATA FROM ANTARCTIC CATCHES

Deriving estimated numbers of young-of-year from pregnancy rate data is relatively simple where gestation periods are 12 months or less and there is strong seasonality in breeding. Where a gestation period of greater than 12 months is expected, however, samples may include months in which both young to be born in that year and young conceived in that year are represented. Inflated estimates of birth rates may be produced. The tendency would be most marked in samples taken over a short period in which overlap may be expected.

Fig. 1 is a schematic representation of a strongly seasonal reproduction pattern with a 3 month breeding season and a 15 month gestation period—one pattern which may be considered for Antarctic killer whales. Killer whales were taken in January, February and March in 1980.

The distribution of 143 foetus lengths is given in Fig. 2. It is clearly bimodal.

Fig. 2b gives % frequency of pregnant females in the 1979/80 Antarctic killer whale catch by length. The significant number of pregnant females below 16 ft should

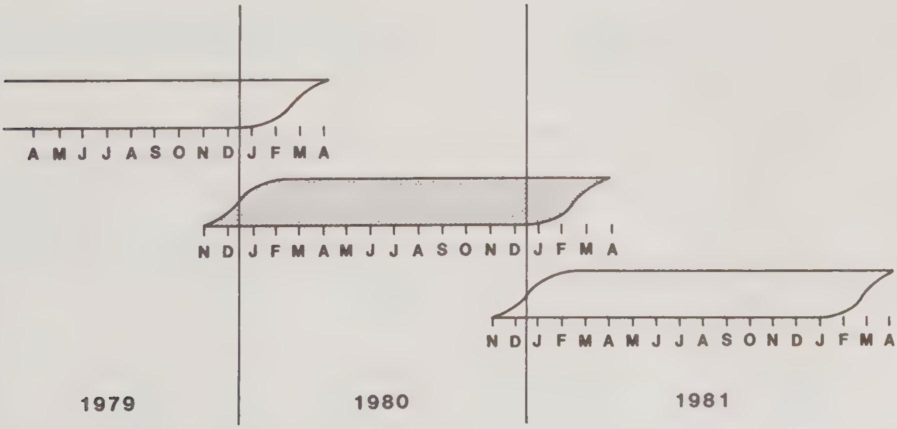
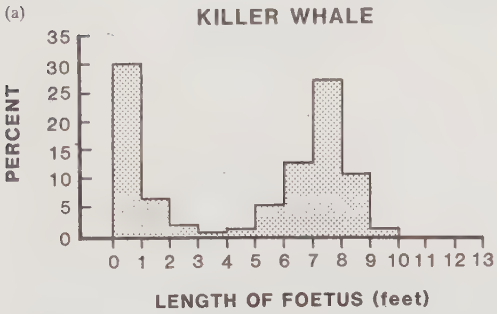

A M J J A S O N D J F M A
N D J F M A M J J A S O N D J F M A
N D J F M A M J J A S O N D J F M A
1979
1980
1981

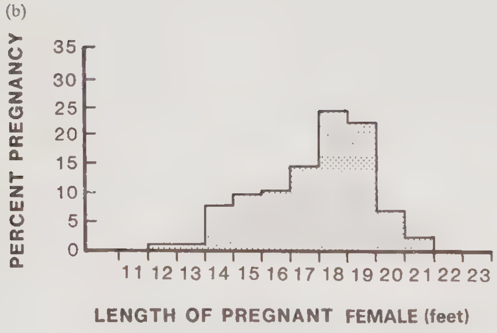
Fig. 1. 3-month breeding period and 15-month gestation.

be noted. No attempt has been made to remove females less than 16 ft from the following calculation.

The bimodal distribution of foetus lengths in Fig. 2a is consistent with a seasonal breeding pattern and a gestation period of more than 12 months as illustrated in Fig. 1. If those assumptions are correct, it is clear that using the overall pregnancy figures will result in an inflated pregnancy rate/female/year and in expected numbers of young-of-year. The bias will be dependent upon the degree of overlap during the sampling period.



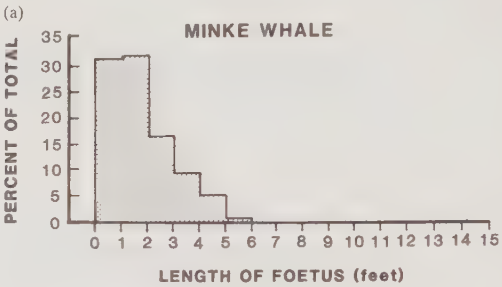
Killer—Antarctic
1979/80
number 143
Jan–March



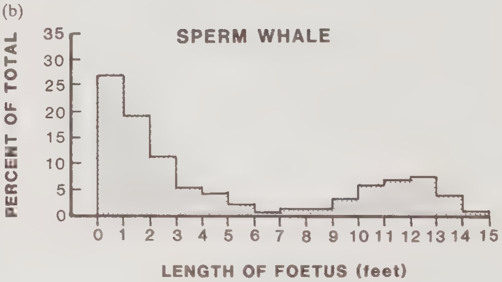
Killer—Antarctic
Length of Pregnant ♀
1979/80

Fig. 2. Distribution of foetus lengths of 143 killer whale foetuses from USSR Antarctic catch 1979/80 (January–March) (a) and length distribution of pregnant females (b).

For comparison, summed foetal length distributions for several seasons are also given for minke whales, with a 12 month gestation period and unimodal length distribution, and for sperm whales, with an approximately 16 month gestation period and a bimodal length distribution (Fig. 3).



Minke—Antarctic
(Number 16760)
1974/75–1979/80
Nov–Feb



Sperm—Antarctic
1973/74–1978/79
n = 650

Fig. 3. Distribution of lengths of 1,670 minke whale foetuses (a) and 650 sperm whale foetuses (b) from Antarctic catches.

Antarctic killer whale catch 1979/80 (BIWS 1980)
From the distribution of foetal lengths in Fig. 2, the number of pregnancies resulting from 1980 impregnations can be gauged from the peak of small foetuses between 0–3 ft. The group of larger foetuses between 5 and 10 ft in length are 1978/79 impregnations near term, and two independent estimates of annual pregnancy rate can thus be obtained (see Table below).

Total catch	Immature ♀	Mature	Total pregnant	To term, 1980	Pregnancy/ mature ♀	To term, 1981	Pregnancy/ mature ♀	Average
916	34	428	143	85	0.199	57	0.133	0.166

Similar considerations apply to the data on pregnancy rates given by Mikhalev and Ivashin (1981) for 123 killer whales taken between November and March in the period 1961/62 to 1978/79. Two hundred and five males and 118 females were taken, 92 of which were examined for pregnancy; one was immature. Without foetal length distributions, it is assumed that only half of the pregnancies would lead to calves in the year of capture and the overall pregnancy rate has been halved to obtain the expected corrected pregnancies and the rate for an individual year per mature female (see Table below).

1961/62–1978/79

Total	Total ♀	Total examined	Mature	Pregnant	Overall rate/female	Corrected pregnancy of year/mature female
323	118	92	91	25	0.274	0.137

NORTHERN HEMISPHERE KILLER WHALE CATCHES

Estimates of pregnancy rates from Norwegian catches of killer whales for the period 1938/67 are given in SC/Jn81/KW4, Table 5 as 13.7%. Pregnancy rates were obtained from whales taken in most months of the year, unlike for the Antarctic catches. Correction of pregnancy rates to avoid the incorporation of more than one cycle of impregnation is less straightforward. As a first approximation, however, a correction may be made by reducing the overall pregnancy rate in proportion to months in which there is likely to be an overlap.

$$Pc = Po - 0.5 \frac{(G - 12)}{12} Po$$

Pc = corrected pregnancy rate.
Po = observed pregnancy rate.
G = gestation period in months (15 months).

$$\begin{aligned} Pc &= 59/430 - 0.5\ 3/12\ (59/430) \\ &= 0.120 \text{ pregnancies/mature female} \end{aligned}$$

Data presented in SC/Jn81/KW1 are difficult to partition for the two years in question; foetuses over 100 cm given as occurring in the later September/February period do not appear in the earlier September/February period in Fig. 6. Conversely, foetuses under 100 cm in length are not reported for the second September/February period. As an approximation, however, if breeding is considered to be seasonal to a degree, with a peak in October/December for conception, then 6 of the 18 months listed will be months in which overlap in reproduction cycles occurs and

$$\begin{aligned} Pc &= 51/129 - 0.5 \times 6/18\ (51/129) \\ &= 0.33 \text{ pregnancies/mature female} \end{aligned}$$

It is clear, however, that catches are not distributed evenly throughout the 18 months given in Fig. 6 of SC/Jn81/KW1, and the pregnancy/mature female can be expected to be less than the initially corrected figure.

No account has been taken in the foregoing of the possibility of proportional over-representation of pregnant females in catches through selection or through avoidance by females with calves of catch vessels. Should that occur, it would further depress the corrected pregnancy rate/mature female.

OBSERVED BIRTH RATES AND CALF RATIOS

Available observed birth rates and calf ratios for the northern Pacific and the Antarctic and their sources are given below

Birth rates			Source
0.089	calves/female/year		SC/Jn81/KW9
0.098	,, ,, ,,	cropped pods	SC/Jn81/KW4
0.069	,, ,, ,,	uncropped pods	

Calf ratios Calves	(Mature?) females	Calves/ female	All other ages		
5	37	0.135	94	cropped pods	SC/Jn81/KW4
3	33	0.091	—	uncropped pods	
6	58?	0.102	147		
51 (7–12 ft)	274	0.186	736	(Antarctic)	SC/32/SM10

In examining the Antarctic data in SC/32/SM10, it is clear that some of the calves present would have been more than one year old on the basis of length. It is also likely that all 1980 calves were not yet born at the time of the survey, and the figure has not been reduced to remove 1+ juveniles. Mature females were taken as 40% of the total number of whales other than calves sighted.

8231

SC/33/SM6

Time/Area Distribution and Composition of the Incidental Kill of Dolphins and Small Whales in the U.S. Purse-Seine Fishery for Tuna in the Eastern Tropical Pacific, 1979–80

W. F. Perrin and C. W. Oliver

Marine Mammal Biology Program, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, California, USA 92038

ABSTRACT

Data are presented for 4,642 spotted dolphins, *Stenella attenuata;* 1,745 spinner dolphins, *S. longirostris;* 99 striped dolphins, *S. coeruleoalba;* 1,535 common dolphins, *Delphinus delphis;* two bottlenose dolphins, *Tursiops truncatus;* one Pacific white-sided dolphin, *Lagenorhynchus obliquidens,* and one false killer whale, *Pseudorca crassidens.* Possible source of biases in the samples are discussed.

INTRODUCTION

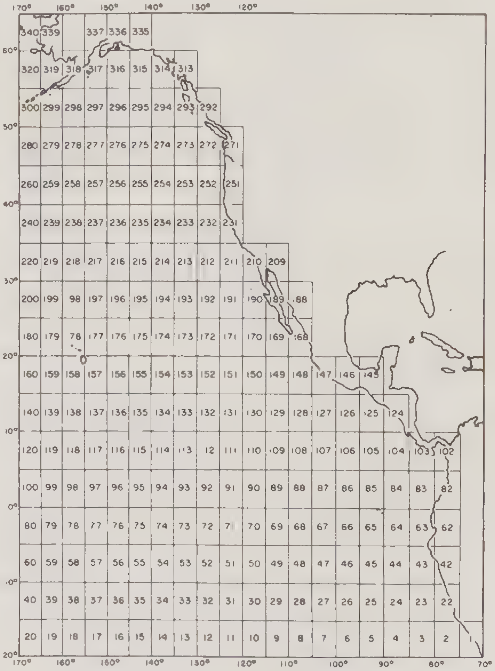
Data on composition of the U.S. incidental purse-seine kill of small cetaceans have been presented and analyzed in a series of publications (Perrin, Coe and Zweifel, 1976; Perrin, Holts and Miller, 1977; Perrin, Miller and Sloan, 1977; Perrin and Henderson, 1979; Smith, 1979; and Henderson, Perrin and Miller, 1980). Recent studies have shown that the data may be subject to biases, of several kinds. The purpose of this paper is to present the data for 1979 and 1980 and to discuss the biases affecting them.

METHODS

The kill data and the life-history specimens from which the data on reproductive condition were derived were collected by fishery technicians employed by the U.S. National Marine Fisheries Service (NMFS) and the Inter-American Tropical Tuna Commission (IATTC) aboard commercial purse-seiners. Data on kill by time and area reported here were collected only by the NMFS technicians. Data on sex composition, reproductive condition and length frequencies of the kill were collected by IATTC and NMFS technicians. NMFS technicians collected data on 62 cruises in 1979 and 41 cruises in 1980. IATTC technicians collected data on 25 cruises in 1979 and 38 in 1980. The sampling scheme is described in Smith (1979), and copies of the forms used are included here as Appendices 1 and 2. Laboratory procedures for processing the specimens and criteria for sexual maturity were as described in Perrin *et al.* (1975 and 1977). The management units used here are defined in Smith (1979). Dolphins not identified to species are not included in the data presented here. The NMFS observed-kill data are presented by 5°-square areas (Fig. 1). The computer programs used to summarize data on reproductive condition were described by Henderson and Perrin (1980).

RESULTS

Incidental kill data by area and month are presented for 8,026 small cetaceans in Tables 1–5. Sex data for 3,408 dolphins, by area and quarter, are presented in Tables 6–10. Length-frequency data for 3,455 specimens are presented in Tables 11–13 and reproductive-condition data for 1,850 females in Tables 14–16. The tables can be found on pp. 000–00.


170° 160° 150° 140° 130° 120°
60° 50° 40° 30° 20° 10° 0° 10° 20°
340 339 337 336 335
320 319 318 317 316 315 314 313
300 299 298 297 296 295 294 293 292
280 279 278 277 276 275 274 273 272 271
260 259 258 257 256 255 254 253 252 251
240 239 238 237 236 235 234 233 232 231
220 219 218 217 216 215 214 213 212 211 210 209
200 199 98 197 196 195 194 193 192 191 190 189 188
180 179 78 177 176 175 174 173 172 171 170 169 168
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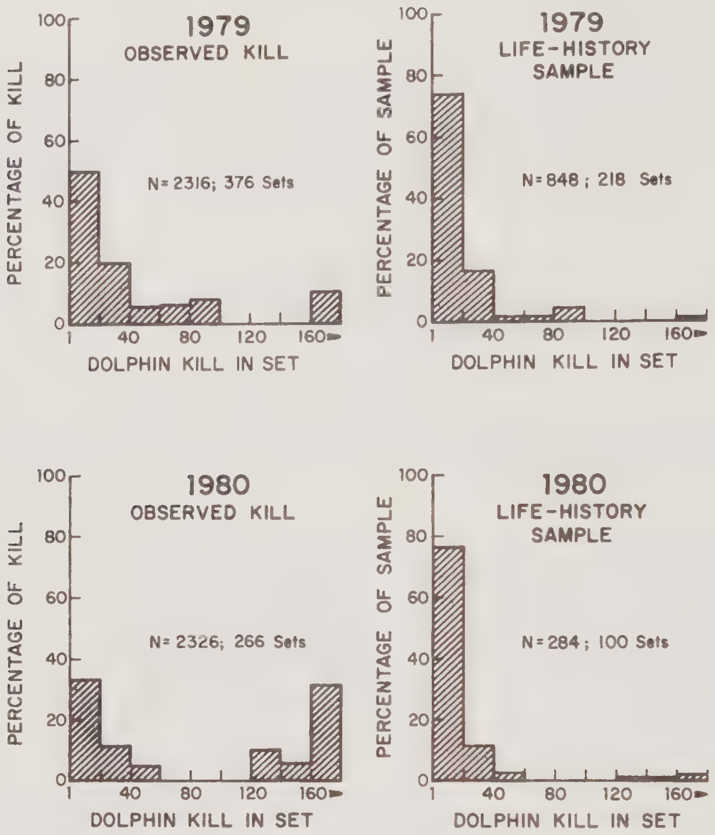
120 119 118 117 116 115 114 113 12 111 110 109 108 107 106 105 104 103 102
100 99 98 97 96 95 94 93 92 91 90 89 88 87 86 85 84 83 82
80 79 78 77 76 75 74 73 72 71 70 69 68 67 66 65 64 63 62
60 59 58 57 56 55 54 53 52 51 50 49 48 47 46 45 44 43 42
40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22
20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1
170° 160° 150° 140° 130° 120° 110° 100° 90° 80° 70°

Fig. 1. Statistical reporting blocks (5-degree squares) for eastern tropical Pacific. Dashed line includes usual area of operation of US tropical-tuna purse-seine fishery (area of consideration for this paper). Solid line includes blocks in which data reported here were collected in 1979 and 1980.



	Spinner dolphin		Common dolphin		Striped dolphin	
	Overall kill	Life-history sample	Overall kill	Life-history sample	Overall kill	Life-history sample
Total sets	285	149	83	47	13	8
Total dolphins	1,745	389	1,535	289	99	30
	(% of kill)	(% of sample)	(% of kill)	(% of sample)	(% of kill)	(% of sample)
Kill in set:						
1–19	42.7	86.6	22.9	57.4	73.7	93.3
20–39	10.7	6.7	10.0	12.8	26.3	6.7
40–59	2.9	2.8	15.1	21.8		
60–79	6.9		4.6			
80–99	5.1	1.3	11.5	1.7		
100–119			7.4	6.2		
120–139						
140–159						
> 160	31.7	2.6	28.5			
Total	100.0	100.0	100.0	100.0	100.0	100.0

Fig. 2. Comparisons of kill-size structures of observed kills with those of subsamples from which life-history data and specimens were collected; for spotted dolphin, *Stenella attenuata*, in 1979 and 1980. Includes only data collected by NMFS technicians. The table compares kill-size structures of observed kill with those of subsamples for which life-history data and specimens were collected (same analysis as in Fig.): for spinner dolphins, *Stenella longirostris*; common dolphin, *Delphinus delphis*; and striped dolphin, *S. coeruleoalba*; 1979 and 1980 combined. Includes only data collected by NMFS observers.

DISCUSSION

Several potential sources of bias have been identified and are discussed below. For some, adjustment procedures have been developed; others have not yet been so addressed.

Effects of size of kill

Powers and Barlow (1979) examined the age structure of kill samples in relation to the size of the kill in the purse-seine set from which the samples came. They found that for the spotted dolphin, *Stenella attenuata,* samples from small-kill sets contained proportionately more calves than did those from large-kill sets. This has been interpreted to mean that calves are more vulnerable to death in the purse-seine operation than are adults, and therefore when only a few animals are killed, they tend to be calves. This would mean that the large-kill samples are more representative of the populations at large (or, at least, the animals captured) than are the small-kill samples. The most recent analyses of data for *S. attenuata* to estimate reproductive rates have taken this presumed effect into account by including only samples from net sets in which 40 or more spotted dolphins were killed (Henderson, Perrin and Miller, 1980). Powers and Barlow (1979) did not find a similar effect for the spinner dolphin, *S. longirostris,* and analyses for that species have been based on all samples regardless of kill size (Perrin and Henderson, 1979). The data for other species (*S. coeruleoalba* and *Delphinus delphis*) have not been examined for the presence of a kill-size effect.

An aspect of the kill-size effect that has not been taken into account relates to the fact that the technicians at sea do not process all dead animals that pass across the deck; they are limited to 30–40 dolphins by constraints of time and space. This means that the animals from small-kill (less than 30–40 sets) are usually all examined, whereas only a subsample of the animals from large-kill sets are examined, amplifying the bias caused by the kill-size effect for *S. attenuata* and possibly for *S. coeruleoalba* and *D. delphinus*. The under-representation of animals from large-kill sets in the life-history samples is shown in Fig. 2.

Effect of seasonality

Perrin *et al.* (1976) and Perrin *et al.* (1977) described diffuse seasonality in breeding of spotted and spinner dolphins in the eastern tropical Pacific, with two or more peak periods during the year. Because of the multiple peaks, the diffuseness, and the fact that the length of gestation is nearly a year (11.5 months in *S. attenuata* and 10.6 months in *S. longirostris*), the effect of seasonal sampling bias (as can be seen in Tables 1–5) on estimates of reproductive rates cannot be large. Barlow (1979) examined the effect of seasonality and developed a method to adjust for it. He found a maximum effect on pregnancy-rate estimates of 4% (for eastern spinner dolphins). Barlow also described variation in seasonal breeding peaks between sub-areas of what have been assumed to be areas containing single interbreeding populations. He concluded that the effect of seasonal-sampling bias on estimates of reproductive rates is probably more than the maximum 4% that he found because of this confounding of breeding units in the analyses. Stuntz (1980) also found areal variation in seasonality, within putative interbreeding populations of the spotted dolphin. This confounding of populations, of course, has other implications for assessment and management. As fishing effort is not evenly distributed by area, the various cryptic subpopulations may differ from each other in status and production.

Other biasing effects

Stuntz (1980) found differences in the age structure of spotted dolphin samples with size of the dolphin school (more calves in smaller schools), tons of yellowfin tuna captured (fewer calves with larger tuna catches) and length of the chasing and corralling phase (see Perrin, 1969, for description of fishing operation) (fewer calves after longer chases) as well as with area and time of year. He pointed out that there are alternative explanations for the observed trends and noted that definitive analyses of the biases must be carried out before the structural (and reproductive) dynamics of the populations can be modeled with any confidence.

ACKNOWLEDGEMENTS

The owners, captains and crews of the U.S. tuna fleet cooperated fully with the collection of data and specimens. We thank them and the many NMFS and IATTC technicians who carried out the field work.

R. B. Miller and V. L. Cass processed the specimens in the laboratory and prepared the data for analysis. M. S. Lowry and T. C. Foster reviewed the final tables. K. S. Raymond prepared the figures, and V. Hostler typed the manuscript.

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Table 1

Kill data for spotted dolphin, *Stenella attenuata*, in observed kill, 1979 and 1980; by stock, five-degree square and month of the year; data collected by NMFS observers on U.S.-registered vessels.

Species and Stock	5-DEG SQUARE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	ALL MONTHS
SPOTTED DOLPHIN:														
Northern Offshore														
1979	83	0	0	0	1	0	0	0	0	0	0	0	0	1
	84	13	0	6	2	0	0	0	0	0	0	0	0	21
	85	24	13	0	0	0	0	0	0	0	0	0	0	37
	86	0	0	0	0	0	0	0	0	0	4	0	0	4
	87	0	0	0	0	0	0	0	0	0	1	0	0	1
	88	0	0	0	0	0	0	0	0	11	0	2	0	13
	90	0	0	0	0	4	0	0	0	0	0	0	0	4
	103	0	1	0	0	0	0	0	0	0	0	0	0	1
	104	40	0	0	4	0	0	0	0	0	0	0	0	44
	105	5	1	0	5	3	0	0	0	0	0	0	0	14
	106	40	1	16	0	0	0	0	0	0	6	0	0	63
	107	30	1	10	0	0	0	0	8	0	265	0	0	314
	108	4	0	0	0	0	0	0	7	0	10	12	0	33
	109	0	0	0	0	0	0	0	0	0	3	0	0	3
	110	0	0	0	0	7	0	0	3	0	0	1	0	11
	111	0	0	0	0	0	3	1	5	1	0	0	0	10
	112	0	0	0	12	80	2	39	0	0	0	0	0	133
	113	0	0	0	0	4	13	6	4	0	0	0	0	27
	114	0	0	0	0	0	72	2	0	0	0	0	0	74
	125	0	4	7	13	62	0	0	0	0	0	0	0	86
	126	20	29	30	1	0	0	2	0	0	0	0	0	82
	127	6	12	13	7	0	0	0	0	0	6	0	0	44
	128	69	4	16	5	4	1	0	2	15	47	0	0	163
	129	0	0	0	1	4	0	0	0	0	0	1	0	6
	130	0	0	0	3	0	0	0	1	0	0	2	0	6
	131	0	0	0	0	0	0	0	27	0	0	0	0	27
	132	0	0	0	0	0	0	12	5	0	0	0	0	17
	133	0	0	0	0	0	1	13	72	3	0	0	0	89
	134	0	0	0	0	0	30	45	2	1	0	0	0	78
	146	0	0	1	2	0	0	0	0	0	0	0	0	3
	147	0	1	0	2	2	0	30	0	1	0	0	0	36
	148	13	18	0	0	0	7	0	0	2	0	1	0	41
	149	23	0	4	6	1	3	3	0	2	2	3	0	47
	150	0	0	0	0	2	0	1	0	0	0	0	0	3
	151	0	0	0	0	20	0	0	0	0	0	0	0	20
	168	0	0	0	0	0	1	0	0	0	0	2	0	3
	170	0	0	0	0	0	0	1	0	0	0	0	0	1
	Total	287	85	103	64	193	133	155	136	36	344	24	0	1560
1980	83	1	0	0	0	0	0	0	0	0	0	0	0	1
	84	0	0	0	0	0	0	0	0	0	6	18	0	24
	85	0	0	0	0	0	0	0	0	0	0	1	0	1
	86	0	7	0	0	0	0	0	0	0	0	0	0	7
	88	0	0	0	0	0	0	0	0	0	3	0	0	3
	89	0	0	0	0	0	0	0	0	0	6	0	0	6
	90	0	0	0	0	0	0	0	0	43	20	0	0	63
	91	0	0	0	0	0	0	0	0	2	13	0	0	15
	104	0	0	248	6	0	0	0	0	0	0	0	0	254
	105	0	0	2	1	8	0	0	0	0	0	2	15	28
	106	125	9	0	0	0	0	0	0	3	0	13	35	185
	107	10	54	3	1	0	0	0	0	0	144	3	0	215
	108	0	0	0	0	0	0	0	2	3	10	9	0	24
	109	0	0	0	0	1	0	0	0	1	0	32	0	34
	110	0	0	0	0	0	0	0	0	0	0	0	1	1
	111	0	0	0	0	0	0	0	0	0	1	0	0	1
	112	0	0	0	0	0	12	11	16	0	0	0	0	39
	113	0	0	0	0	0	8	12	1	0	0	0	0	21
	114	0	0	0	0	0	2	72	3	0	6	0	0	83
	125	5	0	0	0	0	0	0	0	0	0	0	0	5
	126	0	13	1	0	3	0	0	0	0	0	0	0	17
	127	0	4	0	0	0	0	0	0	1	0	0	0	5
	128	1	0	15	42	17	0	0	10	2	0	0	0	87
	129	2	0	15	11	0	1	0	27	1	32	8	0	97
	130	0	0	0	0	0	0	10	0	6	1	0	0	17
	131	0	0	0	0	0	0	2	17	0	8	0	0	27
	132	0	0	0	0	0	4	4	0	0	0	0	0	8
	133	0	0	0	0	0	1	0	0	4	21	0	0	26
	134	0	0	0	0	0	0	4	1	0	0	0	0	5
	147	0	2	0	0	0	0	0	0	0	0	0	0	2
	149	0	0	1	55	0	0	29	10	0	0	0	0	95
	150	0	0	0	0	1	4	2	0	40	0	0	0	47
	168	1	0	0	0	0	0	0	0	0	0	0	0	1
	169	1	0	0	0	0	0	0	0	0	0	0	0	1
	Total	146	89	285	116	30	32	146	87	106	271	86	51	1445
Southern Offshore														
1979	23	2	0	0	0	0	0	0	0	0	0	0	0	2
	24	57	0	0	0	2	0	0	0	0	0	0	0	59
	25	0	0	0	0	0	0	0	0	0	0	0	3	3
	43	9	0	0	0	0	0	0	0	0	0	0	0	9
	44	220	0	0	3	350	1	0	0	0	0	0	0	574
	45	1	0	0	0	0	0	0	0	0	0	0	17	18
	64	1	0	0	0	0	0	0	0	0	0	0	0	1
	65	4	0	0	0	0	0	0	0	0	0	0	0	4
	66	0	36	0	0	0	0	0	0	0	0	0	0	36
	Total	294	36	0	3	352	1	0	0	0	0	0	20	706
1980	23	12	9	0	0	0	0	0	0	0	0	0	0	21
	24	1	2	0	0	0	0	0	0	0	0	0	10	13
	43	165	2	1	0	0	0	0	0	0	0	0	0	168
	44	4	55	2	0	0	0	0	0	0	568	0	0	629
	45	40	0	0	0	0	0	0	0	0	0	0	0	40
	66	1	0	0	0	0	0	0	0	0	0	0	0	1
	Total	223	68	3	0	0	0	0	0	0	568	0	10	872

Table 1—*continued*

Species and Stock	5-DEG SQUARE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	ALL MONTHS
Coastal														
1979	168	0	0	0	40	0	0	0	0	0	0	0	0	40
Unidentified to Stock														
1979	148	0	0	0	0	0	0	0	10	0	0	0	0	10
1980	84	0	0	0	0	0	0	0	0	0	0	0	1	1
	104	0	0	0	0	0	0	0	0	0	0	0	8	8
	Total	0	0	0	0	0	0	0	0	0	0	0	9	9
All Stocks														
1979	Total	581	121	103	107	545	134	155	146	36	344	24	20	2316
1980	Total	369	157	288	116	30	32	146	87	106	839	86	70	2326

Table 2

Kill data for spinner dolphin, *Stenella longirostris*, in observed kill, 1979 and 1980; by stock, five-degree square and month of the year; data collected by NMFS observers on U.S.-registered vessels.

Species and Stock	5-DEG SQUARE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	ALL MONTHS
SPINNER DOLPHIN:														
Northern Whitebelly														
1979	85	6	7	0	0	0	0	0	0	0	0	0	0	13
	86	0	0	0	0	0	0	0	0	0	1	1	0	2
	87	0	0	0	0	0	0	0	0	0	3	0	0	3
	88	0	0	0	1	0	0	0	0	0	0	0	0	1
	89	0	0	0	0	0	0	0	1	0	0	0	0	1
	90	0	0	0	0	1	0	0	0	0	0	0	0	1
	91	0	0	0	1	0	0	0	0	0	0	0	0	1
	106	0	0	4	0	0	0	0	0	0	0	0	0	4
	107	1	0	0	0	0	0	0	0	0	0	0	0	1
	108	2	0	0	3	0	0	0	0	0	2	0	0	7
	109	0	0	0	0	0	0	0	0	0	2	0	0	2
	111	0	0	0	0	0	1	2	2	0	0	0	0	5
	112	0	0	0	0	10	0	0	4	0	0	0	0	14
	113	0	0	0	0	0	2	0	7	0	0	0	0	9
	114	0	0	0	0	0	40	2	0	0	0	0	0	42
	128	1	0	0	0	0	0	0	0	2	0	0	0	3
	131	0	0	0	0	1	0	0	4	0	0	0	0	5
	132	0	0	0	0	0	0	1	3	0	0	0	0	4
	133	0	0	0	0	0	0	9	35	30	0	0	0	74
	134	0	0	0	0	0	12	267	0	0	0	0	0	279
	150	0	0	0	0	0	2	0	0	0	0	0	0	2
	151	0	0	0	0	2	0	0	0	0	0	0	0	2
	Total	10	7	4	5	14	57	281	56	32	8	1	0	475
1980	86	0	14	0	0	0	0	0	0	0	0	0	0	14
	89	0	0	0	0	0	0	0	0	0	2	0	0	2
	90	0	0	0	0	0	0	0	0	2	1	0	0	3
	91	0	0	0	0	0	0	0	0	2	1	0	0	3
	105	0	0	0	0	0	0	0	0	0	0	0	2	2
	107	7	12	0	3	0	0	0	0	0	0	0	0	22
	108	0	0	0	0	0	0	0	0	0	0	1	0	1
	109	0	0	0	0	0	0	0	0	1	0	0	0	1
	111	0	0	0	0	0	0	0	0	0	2	0	0	2
	112	0	0	0	0	0	1	2	9	0	0	0	0	12
	113	0	0	0	0	0	2	2	2	0	1	0	0	7
	114	0	0	0	0	0	2	105	0	0	11	0	0	118
	129	0	0	0	0	0	0	0	0	0	0	7	0	7
	130	0	0	0	0	0	0	4	0	0	0	0	0	4
	131	0	0	0	0	0	2	0	11	0	6	0	0	19
	132	0	0	0	0	0	0	9	0	0	0	0	0	9
	133	0	0	0	0	0	0	0	0	2	2	0	0	4
	134	0	0	0	0	0	0	0	4	0	0	0	0	4
	149	0	0	0	0	0	0	7	0	0	0	0	0	7
	150	0	0	0	0	0	0	0	0	1	0	0	0	1
	Total	7	26	0	3	0	7	129	26	8	26	8	2	242

Table 2—*continued*

Species and Stock	5-DEG SQUARE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	ALL MONTHS
Southern Whitebelly														
1979	24	11	0	0	0	0	0	0	0	0	0	0	0	11
	44	62	0	0	3	116	5	0	0	0	0	0	0	186
	45	9	0	0	0	0	0	0	0	0	0	0	0	9
	46	0	0	0	0	0	0	0	0	0	0	1	0	1
	65	8	0	0	0	0	0	0	0	0	0	0	0	8
	Total	90	0	0	3	116	5	0	0	0	0	1	0	215
1980	23	4	1	0	0	0	0	0	0	0	0	0	0	5
	43	4	0	0	0	0	0	0	0	0	0	0	0	4
	44	1	22	0	0	0	0	0	0	0	286	0	0	309
	Total	9	23	0	0	0	0	0	0	0	286	0	0	318
Eastern														
1979	107	0	0	1	0	0	0	0	0	0	0	0	0	1
	108	0	0	0	0	0	0	0	0	0	6	0	0	6
	109	0	0	0	0	0	0	0	0	0	1	0	0	1
	125	0	2	7	0	0	0	0	0	0	0	0	0	9
	126	1	10	39	0	0	0	26	0	0	0	0	0	76
	127	4	3	94	1	4	0	0	0	0	0	0	0	106
	128	11	2	0	2	1	2	0	0	20	5	0	0	43
	129	0	0	0	0	0	0	0	0	0	0	1	0	1
	133	0	0	0	0	0	0	0	1	0	0	0	0	1
	147	0	1	0	0	0	0	12	0	0	0	0	0	13
	149	0	0	0	1	0	0	0	0	0	0	0	0	1
	150	0	0	0	1	0	0	0	0	0	0	0	0	1
	Total	16	18	141	5	5	2	38	1	20	12	1	0	259
1980	86	0	5	0	0	0	0	0	0	0	0	0	0	5
	125	0	1	9	0	0	0	0	0	0	0	0	0	10
	126	0	1	1	0	3	0	0	0	0	0	0	0	5
	127	0	1	0	0	0	0	0	0	2	0	0	0	3
	128	8	0	17	3	1	0	0	8	0	0	0	0	37
	129	0	0	3	2	1	0	0	0	0	4	16	0	26
	130	0	0	0	0	0	0	0	0	4	0	0	0	4
	131	0	0	0	0	0	0	0	3	0	6	0	0	9
	147	0	3	0	0	0	0	0	0	0	0	0	0	3
	149	0	0	0	0	0	0	0	0	7	1	0	0	8
	Total	8	11	30	5	5	0	0	11	13	11	16	0	110
Unidentified to Stock														
1979	107	3	0	0	0	0	0	0	0	0	0	0	0	3
	108	0	0	0	0	0	0	0	0	0	1	0	0	1
	113	0	0	0	0	0	1	0	0	0	0	0	0	1
	114	0	0	0	0	0	2	0	0	0	0	0	0	2
	126	0	0	1	0	0	0	0	0	0	0	0	0	1
	128	0	0	0	0	0	0	0	0	64	1	0	0	65
	133	0	0	0	0	0	0	1	0	0	0	0	0	1
	148	0	0	0	0	0	0	0	0	0	0	3	0	3
	168	0	0	0	0	0	0	0	0	0	0	1	0	1
	Total	3	0	1	0	0	3	1	0	64	2	4	0	78
1980	114	0	0	0	0	0	0	3	0	0	0	0	0	3
	128	0	0	0	0	0	0	0	2	0	0	0	0	2
	129	0	0	0	0	0	0	0	2	0	5	21	0	28
	130	0	0	0	0	0	0	1	0	0	0	0	0	1
	131	0	0	0	0	0	0	0	5	0	4	0	0	9
	132	0	0	0	0	0	2	2	0	0	0	0	0	4
	150	0	0	0	0	0	0	0	0	1	0	0	0	1
	Total	0	0	0	0	0	2	6	9	1	9	21	0	48
All Stocks														
1979	Total	119	25	146	13	135	67	320	57	116	22	7	0	1027
1980	Total	24	60	30	8	5	9	135	46	22	332	45	2	718

Table 3

Kill data for common dolphin, *Delphinus delphis*, in observed kill, 1979 and 1980; by stock, five-degree square and month of the year; data collected by NMFS observers on U.S.-registered vessels.

Species and Stock	5-DEG SQUARE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	ALL MONTHS
Baja Neritic														
1979	168	0	0	147	490	0	0	0	0	0	0	0	0	637
	169	0	0	0	35	0	0	0	0	0	0	0	0	35
	Total	0	0	147	525	0	0	0	0	0	0	0	0	672
1980	169	13	0	0	0	0	0	0	0	0	0	0	0	13
	189	0	0	0	0	1	0	0	0	0	0	0	0	1
	Total	13	0	0	0	1	0	0	0	0	0	0	0	14
Northern Tropical														
1979	168	2	7	130	13	0	0	0	0	0	0	0	0	152
	169	3	0	0	0	0	0	0	0	0	0	0	0	3
	Total	5	7	130	13	0	0	0	0	0	0	0	0	155
1980	168	6	0	0	0	0	0	0	0	0	0	0	0	6
Central Tropical														
1979	103	14	0	0	0	96	0	0	0	0	0	0	0	110
	104	39	127	178	89	0	0	0	0	0	0	0	0	433
	105	3	0	25	0	0	0	0	0	0	0	0	0	28
	106	0	5	16	0	0	0	0	0	0	0	0	0	21
	125	0	23	0	0	4	0	0	0	0	0	0	0	27
	126	0	9	0	0	0	0	0	0	0	0	0	0	9
	134	0	0	0	0	0	16	0	0	0	0	0	0	16
	Total	56	164	219	89	100	16	0	0	0	0	0	0	644
1980	104	0	0	0	1	0	0	0	0	0	0	0	0	1
	105	0	0	0	0	18	0	0	0	22	2	0	0	42
	Total	0	0	0	1	18	0	0	0	22	2	0	0	43
Southern Tropical														
1979	44	0	0	0	0	1	0	0	0	0	0	0	0	1
All Stocks														
1979	Total	61	171	496	627	101	16	0	0	0	0	0	0	1472
1980	Total	19	0	0	1	19	0	0	0	22	2	0	0	63

Table 4

Kill data for striped dolphin, *Stenella coeruleoalba*, in observed kill, 1979 and 1980; by stock, five-degree square and month of the year; data collected by NMFS observers on U.S.-registered vessels.

Species and Stock	5-DEG SQUARE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	ALL MONTHS
Northern Tropical														
1979	168	0	0	55	2	0	0	0	0	0	0	0	0	57
1980	168	17	0	0	0	0	0	0	0	0	0	0	0	17
Central Tropical														
1979	124	0	0	0	0	0	0	0	0	0	7	0	0	7
	125	0	0	0	18	0	0	0	0	0	0	0	0	18
	Total	0	0	0	18	0	0	0	0	0	7	0	0	25
All Stocks														
1979	Total	0	0	55	20	0	0	0	0	0	7	0	0	82
1980	Total	17	0	0	0	0	0	0	0	0	0	0	0	17

Table 5

Kill data for bottlenose dolphin, *Tursiops truncatus*, Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, and false killer whale, *Pseudorca crassidens*, in observed kill, 1979 and 1980; by five-degree square and month of the year; data collected by NMFS observers on U.S.-registered vessels.

Species	5-DEG SQUARE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	ALL MONTHS
Bottlenosed dolphin														
1979	126	0	1	0	0	0	0	0	0	0	0	0	0	1
	107	0	0	0	0	0	0	0	0	0	1	0	0	1
	Total	0	1	0	0	0	0	0	0	0	1	0	0	2
Pacific white-sided dolphin														
1979	189	0	0	0	0	0	0	0	1	0	0	0	0	1
False killer whale														
1980	126	0	1	0	0	0	0	0	0	0	0	0	0	1

Table 6

Sex data for spotted dolphin, *Stenella attenuata*, in observed kill, 1979 and 1980; by stock, five-degree square and quarter of the year; data collected by IATTC and NMFS observers on U.S.-registered vessels.

Species and Stock	5-DEG SQUARE	QUARTER 1			QUARTER 2			QUARTER 3			QUARTER 4			ALL QUARTERS		
		M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL
Northern Offshore																
1979	66	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
	82	0	0	0	0	0	0	7	9	16	0	0	0	7	9	16
	85	4	9	13	0	0	0	0	0	0	0	0	0	4	9	13
	86	0	0	0	0	0	0	1	0	1	7	16	23	8	16	24
	87	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1
	88	0	0	0	0	0	0	4	4	8	0	1	1	4	5	9
	90	0	0	0	3	0	3	0	1	1	0	0	0	3	1	4
	104	0	1	1	4	0	4	0	0	0	0	0	0	4	1	5
	105	2	4	6	1	6	7	0	0	0	0	0	0	3	10	13
	106	5	19	24	0	0	0	5	5	10	3	2	5	13	26	39
	107	11	10	21	0	0	0	2	4	6	35	55	90	48	69	117
	108	1	3	4	0	0	0	0	0	0	18	27	45	19	30	49
	109	1	8	9	0	0	0	0	0	0	1	1	2	2	9	11
	110	0	0	0	2	0	2	2	1	3	2	5	7	6	6	12
	111	0	0	0	1	0	1	1	0	1	0	0	0	2	0	2
	112	0	0	0	7	12	19	7	11	18	5	5	10	19	28	47
	113	0	0	0	2	5	7	7	8	15	6	2	8	15	15	30
	114	0	0	0	22	26	48	2	1	3	2	9	11	26	36	62
	125	5	5	10	34	29	63	1	0	1	0	0	0	40	34	74
	126	14	23	37	0	1	1	8	3	11	0	0	0	22	27	49
	127	15	27	42	2	3	5	0	0	0	0	3	3	17	33	50
	128	30	28	58	7	23	30	2	3	5	10	18	28	49	72	121
	129	0	0	0	0	4	4	0	0	0	2	7	9	2	11	13
	130	0	0	0	0	0	0	0	0	0	6	10	16	6	10	16
	131	0	0	0	0	0	0	0	0	0	3	0	3	3	0	3
	132	0	0	0	0	0	0	9	9	18	0	8	8	9	17	26
	133	0	0	0	0	0	0	18	29	47	1	2	3	19	31	50
	134	0	0	0	9	18	27	3	5	8	0	0	0	12	23	35
	146	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	147	0	0	0	1	1	2	0	0	0	0	0	0	1	1	2
	148	4	8	12	0	3	3	6	6	12	0	1	1	10	18	28
	149	2	3	5	6	7	13	3	0	3	0	5	5	11	15	26
	150	0	0	0	1	1	2	0	1	1	4	1	5	5	3	8
	151	0	0	0	3	8	11	0	0	0	0	0	0	3	8	11
	168	0	0	0	0	0	0	0	0	0	4	2	6	4	2	6
	Total	94	149	243	105	147	252	89	100	189	109	181	290	397	577	974
1980	66	1	1	2	0	0	0	0	0	0	0	0	0	1	1	2
	83	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	85	1	0	1	3	1	4	0	1	1	14	10	24	18	12	30
	86	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1
	87	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
	88	10	12	22	0	0	0	0	0	0	0	0	0	10	12	22
	89	2	5	7	0	0	0	0	0	0	2	2	4	4	7	11
	90	4	0	4	0	0	0	3	4	7	5	12	17	12	16	28
	91	2	0	2	0	0	0	0	0	0	6	4	10	8	4	12
	104	15	15	30	4	2	6	0	0	0	0	0	0	19	17	36
	105	3	2	5	0	1	1	0	0	0	4	8	12	7	11	18
	106	13	19	32	0	0	0	0	0	0	7	12	19	20	31	51
	107	11	20	31	1	0	1	2	1	3	24	24	48	38	45	83
	108	1	0	1	0	0	0	10	22	32	3	5	8	14	27	41
	109	0	0	0	0	0	0	0	1	1	1	12	13	1	13	14
	111	0	0	0	0	0	0	1	6	7	1	3	4	2	9	11
	112	0	0	0	4	9	13	21	38	59	0	0	0	25	47	72
	113	0	0	0	3	3	6	10	11	21	1	3	4	14	17	31
	114	0	0	0	3	0	3	2	6	8	2	2	4	7	8	15
	125	7	7	14	2	3	5	0	0	0	0	0	0	9	10	19
	126	1	6	7	0	0	0	0	0	0	0	0	0	1	6	7
	127	1	3	4	9	3	12	0	0	0	0	0	0	10	6	16
	128	3	10	13	24	27	51	8	11	19	0	0	0	35	48	83
	129	7	7	14	2	3	5	8	13	21	6	12	18	23	35	58
	130	0	0	0	0	0	0	12	22	34	1	1	2	13	23	36
	131	0	0	0	0	0	0	13	6	19	0	0	0	13	6	19
	132	0	0	0	1	0	1	16	12	28	0	1	1	17	13	30
	133	0	0	0	1	0	1	4	9	13	3	1	4	8	10	18
	134	0	0	0	0	0	0	1	1	2	0	0	0	1	1	2
	148	0	0	0	0	7	7	0	0	0	0	0	0	0	7	7
	149	0	0	0	17	19	36	1	2	3	0	0	0	18	21	39
	150	0	0	0	1	0	1	2	7	9	0	0	0	3	7	10
	169	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	Total	82	109	191	75	78	153	115	173	288	80	113	193	352	473	825
Southern Offshore																
1979	23	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
	24	9	10	19	1	1	2	0	0	0	0	0	0	10	11	21
	25	0	0	0	0	0	0	0	0	0	2	1	3	2	1	3
	43	6	5	11	0	0	0	0	0	0	0	0	0	6	5	11
	44	36	27	63	80	90	170	4	2	6	2	2	4	122	121	243
	45	0	0	0	0	0	0	0	0	0	1	4	5	1	4	5
	64	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	66	13	15	28	0	0	0	0	0	0	0	0	0	13	15	28
	Total	64	58	122	81	91	172	4	2	6	5	8	13	154	159	313
1980	23	2	4	6	0	0	0	0	0	0	0	0	0	2	4	6
	24	0	1	1	0	0	0	0	0	0	4	3	7	4	4	8
	43	19	11	30	0	0	0	0	0	0	0	0	0	19	11	30
	44	8	11	19	0	0	0	0	0	0	5	1	6	13	12	25
	45	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	67	19	26	45	0	0	0	0	0	0	0	0	0	19	26	45
	Total	48	54	102	0	0	0	0	0	0	9	4	13	57	58	115
Coastal																
1979	147	0	0	0	2	5	7	0	0	0	0	0	0	2	5	7
	168	0	0	0	4	8	12	0	0	0	0	0	0	4	8	12
	Total	0	0	0	6	13	19	0	0	0	0	0	0	6	13	19
All Stocks																
1979	Total	158	207	365	192	251	443	93	102	195	114	189	303	557	749	1306
1980	Total	130	163	293	75	78	153	115	173	288	89	117	206	409	531	940

Table 7

Sex data for spinner dolphin, *Stenella longirostris*, in observed kill, 1979 and 1980; by stock, five-degree square and quarter of the year; data collected by IATTC and NMFS observers on U.S.-registered vessels.

Species and Stock	5-DEG SQUARE	QUARTER 1			QUARTER 2			QUARTER 3			QUARTER 4			ALL QUARTERS		
		M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL
Northern Whitebelly																
1979	85	3	1	4	0	0	0	0	0	0	0	0	0	3	1	4
	86	0	0	0	0	0	0	0	0	0	1	1	2	1	1	2
	91	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1
	106	2	2	4	0	0	0	0	0	0	0	0	0	2	2	4
	108	2	0	2	1	1	2	0	0	0	1	3	4	4	4	8
	110	0	0	0	0	0	0	0	0	0	1	2	3	1	2	3
	111	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1
	112	0	0	0	0	0	0	2	2	4	0	0	0	2	2	4
	113	0	0	0	0	1	1	3	4	7	0	0	0	3	5	8
	114	0	0	0	18	18	36	0	2	2	1	0	1	19	20	39
	126	0	2	2	0	0	0	0	0	0	0	0	0	0	2	2
	128	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	132	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1
	133	0	0	0	0	0	0	20	18	38	0	0	0	20	18	38
	134	0	0	0	4	7	11	0	0	0	0	0	0	4	7	11
	150	0	0	0	0	2	2	0	0	0	0	0	0	0	2	2
	Total	7	6	13	24	30	54	25	27	52	4	6	10	60	69	129
1980	85	0	0	0	0	0	0	2	0	2	31	49	80	33	49	82
	88	3	2	5	0	0	0	0	0	0	0	0	0	3	2	5
	89	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
	90	0	0	0	0	0	0	1	0	1	0	1	1	1	1	2
	91	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
	107	2	6	8	1	0	1	0	0	0	0	0	0	3	6	9
	108	0	0	0	0	0	0	3	1	4	0	0	0	3	1	4
	109	0	0	0	0	0	0	0	1	1	1	1	2	1	2	3
	111	0	0	0	0	0	0	3	2	5	1	0	1	4	2	6
	112	0	0	0	2	0	2	3	3	6	0	0	0	5	3	8
	113	0	0	0	0	1	1	1	4	5	0	0	0	1	5	6
	114	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
	128	2	0	2	0	0	0	0	0	0	0	0	0	2	0	2
	129	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1
	130	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1
	131	0	0	0	0	2	2	5	3	8	0	0	0	5	5	10
	132	0	0	0	0	0	0	5	5	10	0	0	0	5	5	10
	133	0	0	0	0	0	0	6	10	16	0	0	0	6	10	16
	134	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1
	Total	7	8	15	3	3	6	32	29	61	33	54	87	75	94	169
Southern Whitebelly																
1979	24	4	3	7	0	0	0	0	0	0	0	0	0	4	3	7
	44	12	10	22	19	13	32	0	0	0	2	0	2	33	23	56
	45	2	3	5	0	0	0	0	0	0	0	0	0	2	3	5
	Total	18	16	34	19	13	32	0	0	0	2	0	2	39	29	68
1980	23	17	12	29	0	0	0	0	0	0	0	0	0	17	12	29
	43	1	1	2	0	0	0	0	0	0	0	0	0	1	1	2
	44	5	3	8	0	0	0	0	0	0	6	4	10	11	7	18
	66	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1
	67	2	1	3	0	0	0	0	0	0	0	0	0	2	1	3
	Total	26	17	43	0	0	0	0	0	0	6	4	10	32	21	53
Eastern																
1979	106	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1
	107	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1
	108	0	0	0	0	0	0	0	0	0	1	8	9	1	8	9
	109	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
	110	0	0	0	0	0	0	0	0	0	1	1	2	1	1	2
	125	5	6	11	0	1	1	0	0	0	0	0	0	5	7	12
	126	13	16	29	0	0	0	6	4	10	0	0	0	19	20	39
	127	33	25	58	0	2	2	5	1	6	0	0	0	38	28	66
	128	11	12	23	2	1	3	3	5	8	4	5	9	20	23	43
	130	0	0	0	0	0	0	0	0	0	7	5	12	7	5	12
	131	5	8	13	0	0	0	1	0	1	1	0	1	7	8	15
	132	0	0	0	0	0	0	0	0	0	3	6	9	3	6	9
	133	0	0	0	0	0	0	1	0	1	1	1	2	2	1	3
	146	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1
	Total	67	68	135	2	4	6	18	10	28	19	26	45	106	108	214
1980	109	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
	125	3	3	6	0	0	0	0	0	0	0	0	0	3	3	6
	126	5	2	7	2	0	2	0	0	0	0	0	0	7	2	9
	127	0	3	3	0	1	1	0	0	0	0	0	0	0	4	4
	128	3	10	13	1	1	2	6	6	12	0	0	0	10	17	27
	129	0	1	1	2	2	4	0	0	0	6	4	10	8	7	15
	130	0	0	0	0	0	0	3	5	8	1	1	2	4	6	10
	131	0	0	0	0	0	0	3	0	3	0	0	0	3	0	3
	132	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1
	133	0	0	0	0	0	0	2	0	2	0	0	0	2	0	2
	149	0	0	0	0	0	0	3	2	5	0	0	0	3	2	5
	Total	11	19	30	5	4	9	17	14	31	8	5	13	41	42	83

Table 7—*continued*

Species and Stock	5-DEG	QUARTER 1			QUARTER 2			QUARTER 3			QUARTER 4			ALL QUARTERS		
	SQUARE	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL
Unidentified to Stock																
1979	107	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
	130	0	0	0	0	0	0	0	0	0	1	1	2	1	1	2
	132	0	0	0	0	0	0	0	0	0	0	2	2	0	2	2
	133	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1
	168	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
	Total	0	0	0	0	0	0	0	0	0	2	5	7	2	5	7
1980	128	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1
	129	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
	131	0	0	0	0	0	0	2	3	5	0	1	1	2	4	6
	132	0	0	0	0	0	0	2	0	2	0	0	0	2	0	2
	133	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1
	Total	0	0	0	0	1	1	5	3	8	1	1	2	6	5	11
All Stocks																
1979	Total	92	90	182	45	47	92	43	37	80	27	37	64	207	211	418
1980	Total	44	44	88	8	8	16	54	46	100	48	64	112	154	162	316

Table 8

Sex data for common dolphin, *Delphinus delphis*, in observed kill, 1979 and 1980; by stock, five-degree square and quarter of the year; data collected by NMFS observers on U.S.-registered vessels.

Species and Stock	5-DEG	QUARTER 1			QUARTER 2			QUARTER 3			QUARTER 4			ALL QUARTERS		
	SQUARE	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL
COMMON DOLPHIN:																
Baja Neritic																
1979	168	4	9	13	16	21	37	0	0	0	0	0	0	20	30	50
1980	169	2	4	6	0	0	0	0	0	0	0	0	0	2	4	6
Northern Tropical																
1979	168	30	28	58	5	3	8	0	0	0	0	0	0	35	31	66
	169	1	1	2	0	0	0	0	0	0	0	0	0	1	1	2
	Total	31	29	60	5	3	8	0	0	0	0	0	0	36	32	68
1980	168	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1
	169	6	6	12	0	0	0	0	0	0	0	0	0	6	6	12
	Total	7	6	13	0	0	0	0	0	0	0	0	0	7	6	13
Central Tropical																
1979	103	10	4	14	3	3	6	0	0	0	0	0	0	13	7	20
	104	20	27	47	37	45	82	0	0	0	0	0	0	57	72	129
	105	0	3	3	0	0	0	0	0	0	0	0	0	0	3	3
	106	6	7	13	0	2	2	0	0	0	0	0	0	6	9	15
	125	3	3	6	7	11	18	0	0	0	0	0	0	10	14	24
	126	7	2	9	0	0	0	0	0	0	0	0	0	7	2	9
	134	0	0	0	1	2	3	0	0	0	0	0	0	1	2	3
	Total	46	46	92	48	63	111	0	0	0	0	0	0	94	109	203
1980	104	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1
	105	0	0	0	4	11	15	0	0	0	0	0	0	4	11	15
	Total	0	0	0	5	11	16	0	0	0	0	0	0	5	11	16
Southern Tropical																
1979	64	3	4	7	0	0	0	0	0	0	0	0	0	3	4	7
All Stocks																
1979	Total	84	88	172	69	87	156	0	0	0	0	0	0	153	175	328
1980	Total	9	10	19	5	11	16	0	0	0	0	0	0	14	21	35

Table 9

Sex data for striped dolphin, *Stenella coeruleoalba*, in observed kill, 1979 and 1980; by stock, five-degree square and quarter of the year; data collected by NMFS observers on U.S.-registered vessels.

Species and Stock	5-DEG SQUARE	QUARTER 1			QUARTER 2			QUARTER 3			QUARTER 4			ALL QUARTERS		
		M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL
Northern Tropical																
1979	168	14	12	26	1	5	6	0	0	0	0	0	0	15	17	32
1980	149	0	0	0	11	4	15	0	0	0	0	0	0	11	4	15
	168	1	8	9	0	0	0	0	0	0	0	0	0	1	8	9
	Total	1	8	9	11	4	15	0	0	0	0	0	0	12	12	24
Central Tropical																
1979	124	0	0	0	0	1	1	0	0	0	1	2	3	1	3	4
	125	0	0	0	5	0	5	0	0	0	0	0	0	5	0	5
	Total	0	0	0	5	1	6	0	0	0	1	2	3	6	3	9
All Stocks																
1979	Total	14	12	26	6	6	12	0	0	0	1	2	3	21	20	41
1980	Total	1	8	9	11	4	15	0	0	0	0	0	0	12	12	24

Table 10

Sex data for bottlenose dolphin, *Tursiops truncatus*, Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, rough-toothed dolphin, *Steno bredanensis*, and false killer whale, *Pseudorca crassidens*, in observed kill, 1979 and 1980; by five-degree square and quarter of the year, data collected by IATTC and NMFS observers on U.S.-registered vessels.

Species	5-DEG SQUARE	QUARTER 1			QUARTER 2			QUARTER 3			QUARTER 4			ALL QUARTERS		
		M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL	M	F	TOTAL
Bottlenosed dolphin																
1979	107	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
	126	1	1	2	0	0	0	0	0	0	0	0	0	1	1	2
	Total	1	1	2	0	0	0	0	0	0	1	0	1	2	1	3
Rough-toothed dolphin																
1979	124	0	0	0	0	0	0	1	3	4	0	0	0	1	3	4
Pacific white-sided dolphin																
1979	189	0	0	0	0	0	0	1	1	2	0	0	0	1	1	2
False killer whale																
1980	126	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1

Table 11

Length frequencies for spotted dolphins, *Stenella attenuata*, and striped dolphins, *Stenella coeruleoalba*, in observed kill, 1979 and 1980; by stock, year, and sex; data collected by IATTC and NMFS observers on U.S.-registered vessels.

Length (cm)	Spotted dolphins										Striped dolphins					
	Northern Offshore				Southern Offshore				Coastal		Central Tropical		Northern Tropical			
	1979		1980		1979		1980		1979		1979		1979		1980	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
75-79		1														
80-84	3					1										
85-89	3	3		3	3	1										
90-94	4	3	2		4	7			1							
95-99	2	8	4	4	4	3		1	1	1						
100-104	2	2		3	3		1			1						
105-109	1	5	5	5		2										
110-114	1	2	2	3	2									1		
115-119	3	2	3	2		1		1								
120-124	5	3	2	2			1					1				
125-129	3	4	5	5	3	2	1									
130-134	4	3	4	3	3		1									
135-139	6	12	8	5	2	1										
140-144	7	11	6	5	2	4										
145-149	8	12	11	5	4	3	1	1								1
150-154	7	18	16	8	6	3	1	2	1							
155-159	24	13	24	20	10	8	2	2								
160-164	36	34	31	31	12	7	2	3						1		
165-169	30	36	32	37	8	9	5	2								
170-174	35	32	23	35	8	18	5	3	1							
175-179	23	50	29	37	18	11	4	5	1				1	2		
180-184	23	69	18	54	11	25	10	5				1	1	1	1	
185-189	22	96	23	75	9	25	7	16			1		1	1	1	
190-194	23	91	30	81	9	15	5	11			1			1	1	3
195-199	42	50	29	44	8	7	4	5	1	1	1		1	3	2	2
200-204	26	16	21	14	13	2	6	1		2		1	3	3	4	3
205-209	28	2	19	2	5	1	1	1					2	2	2	2
210-214	18	1	9	2	5	1					1		3	2	1	1
215-219	7		7	2			1			1	1					
220-224	2		3	1	1					1	1		2			
225-229	2		2										1			
230-234										1						
235-239																
240-244										1						
Total	400	579	368	488	153	157	58	59	6	9	6	3	15	17	12	12

Table 12

Length frequencies for spinner dolphins *Stenella longirostris*, in the observed kill, 1979 and 1980; by stock, year, and sex; data collected by IATTC and NMFS observers on U.S.-registered vessels.

Length (cm)	Northern Whitebelly				Southern Whitebelly				Eastern				Unidentified			
	1979		1980		1979		1980		1979		1980		1979		1980	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
75-79																
80-84	1	1		1												
85-89					2	1				1						
90-94														1		
95-99							2				1					
100-104									1					1		
105-109				1				1				1	1			1
110-114									1	2						
115-119					4				2		1					
120-124	2	2	3	1					4	3		2				
125-129		2	1	2			1		2	3		1				
130-134	4	2	2				1	1		2						1
135-139	1		2	5	2				5	3	1	1				1
140-144	1		1		1			1	3	5		2			1	
145-149	4	2	3	1			2		7	5	2				1	
150-154	3	2	4	6	3		1	1	10	8	5	5		2		
155-159	4	2	3	5		3			13	11	3	5	1	1	2	2
160-164	3	13	2	7	4	2	3	1	13	12	5	4				
165-169	2	6	9	13	1	4	2	4	7	15	6	4				
170-174	5	11	13	20	3	5	7	2	16	18	6	6			1	
175-179	13	12	16	17	5	6	3	4	10	14	7	9			1	
180-184	8	7	10	13	11	4	2		13	9	1	2				
185-189	4	4	7	5	2	4	6	3	4		2					
190-194	5	2	2		1			3			1					
195-199		1					2									
200-204			1													
205-209							1									
210-214																
215-219																
220-224																
225-229																
230-234																
235-239							1									
Total	60	69	79	97	39	29	34	21	111	111	41	42	2	5	6	5

Table 13

Length frequencies for common dolphin, *Delphinus delphis*, in the observed kill, 1979 and 1980; by stock, year and sex; data collected by IATTC and NMFS observers on U.S.-registered vessels.

Length (cm)	Baja Neritic 1979		Baja Neritic 1980		Northern Tropical 1979		Northern Tropical 1980		Southern Tropical 1979		Central Tropical 1979		Central Tropical 1980	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F
75-79														
80-84														
85-89														
90-94											2	1		
95-99														
100-104											1	1		1
105-109														
110-114														
115-119														1
120-124													1	
125-129														
130-134												1		
135-139					1				1					
140-144												1		
145-149					2	2					1			
150-154	1			1		1					2			
155-159	2	1			1				1		4	2		1
160-164		1			2	4			1		1	5		1
165-169	1	1				1	1	1		1	5	5		
170-174	2	5			1	2	1	1		1	6	11		1
175-179	2	11		2	1	7	3	1			4	7		
180-184	4	4			3	8		2		2	8	5		
185-189	2	5			9	3					10	9	1	
190-194	2	2	1	1	6	4					10	20		3
195-199	2		1		7		1				9	20		1
200-204	2				3		1				7	10	1	2
205-209											9	7	1	
210-214											9	2		
215-219											5			
220-224											3		1	
225-229														
230-234														
235-239														
Total	20	30	2	4	36	32	7	5	3	4	94	109	5	11

Table 14

Reproductive condition for 1,276 female spotted dolphins, *Stenella attenuata*, and 17 female striped dolphins, *Stenella coeruleoalba*, in the observed kill, 1979 and 1980; by stock and year; data collected by IATTC and NMFS observers on U.S.-registered vessels.

	Spotted								Striped	
	Northern Offshore 1979		Northern Offshore 1980		Southern Offshore 1979		Southern Offshore 1980		Northern Tropical 1979	
	N	%	N	%	N	%	N	%	N	%
Maturity undetermined	247	42.8	237	49.2	81	51.7	35	60.4	2	11.8
Sexually immature	123	21.2	105	21.8	17	10.8	6	10.3	8	47.0
Sexually mature:										
Condition undetermined	2	0.3	1	0.2	0	0.0	0	0.0	0	0.0
Pregnant only	42	7.3	30	6.2	9	5.7	6	10.3	0	0.0
Pregnant and lactating	17	2.9	9	1.9	1	0.6	0	0.0	0	0.0
Lactating only	117	20.2	75	15.6	28	17.8	8	13.8	3	17.6
"Resting"										
With corpus luteum	7	1.2	6	1.2	10	6.4	0	0.0	0	0.0
Without corpus luteum	21	3.6	19	3.9	10	6.4	3	5.2	4	23.6
Post-reproductive	3	0.5	0	0.0	1	0.6	0	0.0	0	0.0
Total	579	100.0	482	100.0	157	100.0	58	100.0	17	100.0

Table 15

Reproductive condition for 369 female spinner dolphins, *Stenella longirostris*, in the observed kill, 1979 and 1980; by stock and year; data collected by IATTC and NMFS observers on U.S.-registered vessels.

	Eastern				Whitebelly							
					Northern				Southern			
	1979		1980		1979		1980		1979		1980	
	N	%	N	%	N	%	N	%	N	%	N	%
Maturity undetermined	43	38.8	21	50.0	18	26.1	61	62.9	18	62.1	14	66.6
Sexually immature	36	32.4	12	28.6	20	29.1	19	19.6	6	20.7	3	14.3
Sexually mature:												
Condition undetermined	0	0.0	0	0.0	1	1.4	0	0.0	0	0.0	1	4.8
Pregnant only	14	12.6	4	9.5	4	5.8	2	2.1	3	10.3	0	0.0
Pregnant and lactating	0	0.0	0	0.0	1	1.4	1	1.0	0	0.0	0	0.0
Lactating only	15	13.5	5	11.9	12	17.4	10	10.3	2	6.9	3	14.3
"Resting"												
With corpus luteum	0	0.0	0	0.0	6	8.7	0	0.0	0	0.0	0	0.0
Without corpus luteum	3	2.7	0	0.0	7	10.1	4	4.1	0	0.0	0	0.0
Post-reproductive	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Total	111	100.0	42	100.0	69	100.0	97	100.0	29	100.0	21	100.0

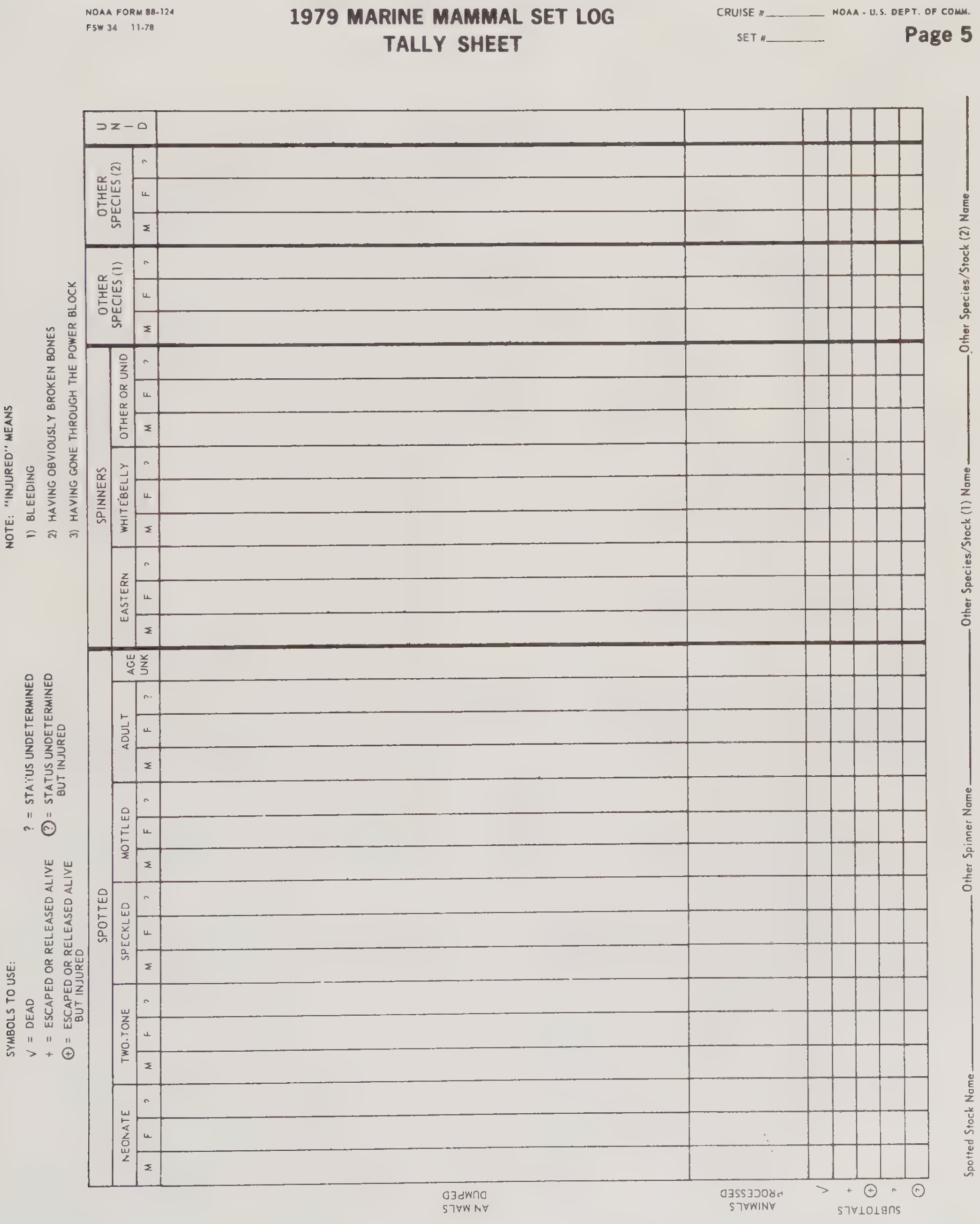
Table 16

Reproductive condition for 188 female common dolphins, *Delphinus delphis*, in the observed kill, 1979 and 1980; by stock and year; data collected by IATTC and NMFS observers on U.S.-registered vessels.

	Baja Neritic		Northern Tropical		Southern Tropical				Central Tropical			
	1979		1979		1979		1980		1979		1980	
	N	%	N	%	N	%	N	%	N	%	N	%
Maturity undetermined	20	66.7	20	62.6	0	0.0	0	0.0	33	30.9	0	0.0
Sexually immature	2	6.7	3	9.4	2	50.0	2	50.0	31	29.0	5	45.4
Sexually mature:												
Condition undetermined	0	0.0	0	0.0	0	0.0	0	0.0	1	0.9	0	0.0
Pregnant only	2	6.7	1	3.1	0	0.0	0	0.0	7	6.5	1	9.1
Pregnant and lactating	0	0.0	1	3.1	0	0.0	0	0.0	4	3.7	0	0.0
Lactating only	4	13.3	6	18.7	2	50.0	2	50.0	22	20.6	4	36.4
"Resting"												
With corpus luteum	1	3.3	1	3.1	0	0.0	0	0.0	3	2.8	0	0.0
Without corpus luteum	1	3.3	0	0.0	0	0.0	0	0.0	6	5.6	1	9.1
Post-reproductive	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Total	30	100.0	32	100.0	4	100.0	4	100.0	107	100.0	11	100.0

Appendix 1

FORM USED BY NMFS TECHNICIANS TO COLLECT INCIDENTAL-KILL DATA ABOARD COMMERCIAL TUNA PURSE-SEINERS



NOAA FORM 88-124
FSW 34 11-78

1979 MARINE MAMMAL SET LOG
TALLY SHEET

CRUISE #________ NOAA - U.S. DEPT. OF COMM.
SET #________

Page 5

SYMBOLS TO USE:
√ = DEAD
+ = ESCAPED OR RELEASED ALIVE
⊕ = ESCAPED OR RELEASED ALIVE BUT INJURED
? = STATUS UNDETERMINED
?⃝ = STATUS UNDETERMINED BUT INJURED

NOTE: "INJURED" MEANS
1) BLEEDING
2) HAVING OBVIOUSLY BROKEN BONES
3) HAVING GONE THROUGH THE POWER BLOCK

	SPOTTED																SPINNERS									OTHER SPECIES (1)			OTHER SPECIES (2)			UNID
	NEONATE			TWO-TONE			SPECKLED			MOTTLED			ADULT			AGE UNK	EASTERN			WHITEBELLY			OTHER OR UNID									
	M	F	?	M	F	?	M	F	?	M	F	?	M	F	?		M	F	?	M	F	?	M	F	?	M	F	?	M	F	?	
ANIMALS DUMPED																																
ANIMALS PROCESSED																																
SUBTOTALS √																																
+																																
⊕																																
?																																
?⃝																																

Spotted Stock Name________ Other Spinner Name________ Other Species/Stock (1) Name________ Other Species/Stock (2) Name________

Appendix 2

FORM USED BY NMFS AND IATTC FIELD AND LABORATORY TECHNICIANS TO COLLECT LIFE-HISTORY DATA ON DOLPHINS KILLED IN THE TUNA PURSE-SEINE FISHERY

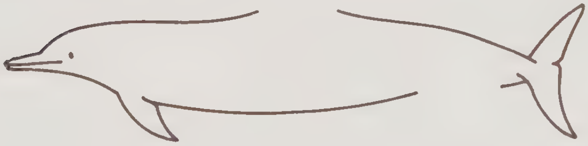
NOAA FORM 88-129
NMFS 11/80

PORPOISE LIFE HISTORY FORM

NOAA
U.S. DEPT. OF COMM.

CARD 1 (12)

CR. # ______ (1–4)   SPECIMEN # ______ (5–12)
SPECIES/STOCK ______ (13 14)   SEX ______ (15)
DATE (YR/MO/DAY) ______ (16–21)   SET # ______ (22–24)
POSITION (LAT/LONG) ______ (25–33)   QUAD ______ (34)
TOTAL LENGTH (cm.) ______ (35–38)   COLORATION ______ (39)
LACTATING ? ______ (40)   FETUS: SEX ______ (41)   LENGTH (cm.) ______ (42–45)
COLLECTED ?: TEETH ______ (46)   TESTIS ______ (47)   OVARIES & UTERUS ______ (48)
FETUS ______ (49)   STOMACH ______ (50)   HEAD ______ (51)   CARCASS ______ (52)
PHOTOS ? ______ (53)   ROLL # ______   FRAME(S) # ______
COLOR PATTERN & DORSAL FIN: BASIS FOR STOCK ID.:



______ (OBSERVER'S NAME)

IN FIELD ↑

NOTE: IF FETUS < 25 CM., LEAVE IN UTERUS & PRESERVE (do not sex & measure in field)

IN LAB ↓

54 TOTAL WEIGHT (gm)	61 Lt. GONAD (gm) 67	68 Rt. GONAD (gm) 74	75 Ln (mm)	S.G.	E	80 BL
			RIGHT TESTIS			

1 REPEAT COLS. 1-11, CARD 1 11	CARD 2 12	13 LAYERS 15	16 C.L.	17 1	19 2	21 3	23 CA (L)	25 CA (R)
				C.L. DIAMS. (mm)				

27 FOLL. DIAM. (mm)	30 1	32 2	34 3	36 4	38 5	40 6	42 1	44 2	46 3	48 4	50 5	52 6	54 Total CORP. (C.A.+C.L.)
	C.A. IN LEFT OVARY						C.A. IN RIGHT OVARY						

56 TUBULE DIAM. (mm)	59 FETUS WEIGHT (gm)	66 READING STATUS	68 READER CODE

C. A. diams. (mm), by Type

1	2	3	4	5	6

NOTES (Uterus, Etc.):

DISPOSITION OF MATERIALS:

8232

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STATUS OF POPULATIONS OF SPOTTED DOLPHIN, *STENELLA ATTENUATA*, AND SPINNER DOLPHIN, *S. LONGIROSTRIS*, IN THE EASTERN TROPICAL PACIFIC

W.F. Perrin, T.D. Smith and G.T. Sakagawa

Abstract

This paper reports progress on assessing the status of three populations of two species of dolphins of the genus *Stenella* involved in the purse-seine fishery for tuna in the eastern tropical Pacific Ocean. The types of data used, the methods used to collect and analyse them and the main assumptions and other sources of uncertainty in the study – as well as the measures taken in some cases to account for these – are summarized.

The size of the population of offshore spotted dolphins (*S. attenuata* sub-species) in 1974 was first estimated to be 2.3-4.9 million, based on an aerial survey. The annual capacity for increase (total births minus natural deaths) was estimated to be 1.4-4.0 %, and the annual rate of observed incidental mortality, based on an estimated kill in 1974 of 79 900-97 300 animals, was estimated to be 1.6-4.2 %. Comparison of these rates indicated that the number of spotted dolphins killed in the fishery in 1974 was at or near the population available after natural mortality. Revised estimates for 1974 give a population size between 3.1-3.5 million dolphins (a preferred, central estimate from a larger range), of which 72 000 were killed in the tuna fishery – this gives an incidental fishing mortality rate of 2.1-2.3 %. This rate was compared with the annual capacity for increase as originally estimated and with an independently figured estimate of the incidental mortality rate the population could tolerate. The population size of a second dolphin involved in the tuna fishery, the eastern spinner dolphin (*S. longirostris* sub-species) was given in revised estimates to be between 1.1-1.2 million (also a preferred, central estimate). The number of animals killed incidentally in 1974 was estimated to be 21 000 animals. The resulting incidental mortality rate, 1.8-1.9 %, was compared with an estimated annual reproductive rate of 8.3 %, the low value of which indicates no apparent response of the population to exploitation. For both the offshore spotted dolphin and the eastern spinner dolphin, the revised estimates indicate that if the sizes of their populations were increasing or decreasing under the levels of fishing mortality in 1974, they were probably doing so at low rates. The impact of the tuna fishery on the whitebelly spinner population (*S. longirostris* sub-species) has not yet been assessed. There is a need for increased acquisition of relevant biological and catch data, expanded surveys of population size and estimation of certain life history parameters.

Résumé

Les auteurs rendent compte des progrès accomplis dans l'évaluation de l'état de trois populations de deux espèces de dauphins du genre *Stenella* touchées par la pêche des thonidés à la senne coulissante dans le secteur est du Pacifique tropical. Un résumé porte sur les types

de données utilisées ainsi que leurs méthodes de rassemblement et d'analyse, les principales hypothèses et les autres sources d'incertitude, de même que les mesures prises dans certains cas pour en tenir compte.

La population de dauphins tachetés (sous-espèce de *S. attenuata*) du large a d'abord été estimée en 1974 à 2,3-4,9 millions d'animaux d'après une enquête aérienne. La capacité annuelle d'accroissement (nombre total des naissances moins nombre de morts naturelles) était estimée à 1,4-4 % et le taux annuel de la mortalité accidentelle observée, fondé sur une estimation des morts de 79 900-97 300 animaux en 1974, était évalué à 1,6-4,2 %. La comparaison de ces taux indique que le nombre de dauphins tachetés tués dans les pêches en 1974 était égal ou presque égal à l'excédent de production. La révision des estimations pour 1974 fait apparaître une taille de population de 3,1-3,5 millions de dauphins (estimation centrale préférentielle dans une gamme plus large), dont 72 000 étaient tués dans les opérations de pêche au thon – ce qui donne un taux de mortalité par pêche accessoire de 2,1-2,3 %. Ce taux a été comparé à la capacité annuelle d'accroissement estimée à l'origine et avec une évaluation chiffrée, indépendante, du taux de mortalité accessoire que la population peut supporter. La taille de la population d'un second dauphin touché par la pêche au thon, le dauphin à long bec (sous-espèce de *S. longirostris*), a été indiquée, dans des estimations révisées, comme étant de 1,1-1,2 million d'animaux (ici aussi, une estimation centrale préférentielle). Le nombre de dauphins tués accessoirement en 1974 était estimé à 21 000. Le taux de mortalité accessoire qui en résulte (1,8-1,9 %) a été comparé à l'estimation du taux annuel de reproduction de 8,3 % dont la faible valeur indique que la population ne réagit apparemment pas à l'exploitation. Pour les deux espèces de dauphins, les estimations révisées indiquent que si la taille de leur population augmentait ou diminuait, compte tenu des niveaux de mortalité par capture de 1974, ces taux étaient probablement faibles. On n'a pas encore évalué l'impact de la pêche au thon sur la population de dauphins "white belly" à long bec (sous-espèce de *S. longirostris*). Il est nécessaire de rassembler un plus grand nombre de données sur la biologie et les captures, d'élargir les enquêtes sur la taille des populations et d'effectuer l'estimation de certains paramètres du cycle biologique.

Extracto

Se informa sobre los progresos realizados en la evaluación de la situación de tres poblaciones de dos especies de delfines del género *Stenella* que se capturan accidentalmente en la pesquería de cerco de atún de la parte oriental del Pacífico tropical. Se resumen los datos utilizados, los métodos empleados para recogerlos y analizarlos y las principales hipótesis y otras fuentes de incertidumbre, así como las medidas tomadas en algunos casos para tener estas últimas en cuenta.

La población de delfines moteados de media altura (subespecie de *S. attenuata*) se estimó en 1974, por primera vez, en 2,3-4,9 millones, sobre la base de un reconocimiento aéreo. La capacidad anual de aumento (nacimientos totales menos muertes naturales) se estimó en 1,4-4,0 por ciento, y el índice anual de mortalidad accidental se ha calculado en 1,6-4,2 por ciento, sobre la base de las estimaciones de los animales muertos accidentalmente en 1974 (79 900-97 300). Comparando esos índices se llega a la conclusión de que el número de delfines moteados que se capturaron en la pesquería en 1974 correspondía a la producción excedentaria o se acercaba mucho a ella. Las estimaciones revisadas correspondientes a 1974 arrojan una población de 3,1 a 3,5 millones de delfines (estimación central, preferida, obtenida a partir de una zona de distribución más amplia), de los que 72 000 resultaron muertos en la pesquería de atún, lo que da una mortalidad accidental por pesca de 2,1-2,3 por ciento. Se comparó luego ese índice con la capacidad anual de aumento tal como se había estimado originalmente y con una estimación hecha independientemente de la mortalidad accidental que la población podría tolerar. Por lo que se refiere a la población del otro delfín que se encuentra también en la pesquería de atún, el delfín hilador oriental (subespecie de *S.*

longirostris), las estimaciones revisadas de su población arrojan cifras de 1,1-2,1 millones (se trata también de una estimación central). El número de animales que murieron accidentalmente en 1974 se ha estimado en 21 000. La mortalidad accidental consiguiente (1,8-1,9 por ciento) se comparó con un índice anual estimado de reproducción de 8,3 por ciento, que, al ser tan bajo, indica que no existe respuesta aparente de la población a la explotación. Tanto por lo que se refiere al delfín moteado como al delfín hilador oriental, las estimaciones revisadas indican que, si en 1974 la población estaba aumentando o disminuyendo por debajo de los límites de mortalidad por pesca, probablemente ese aumento o disminución era muy lento. Las repercusiones de la pesquería de atún en la población de delfín hilador de vientre blanco (subespecie de *S. longirostris*) no se han evaluado aún. Es necesario recoger más datos biológicos y de captura, hacer más reconocimientos de la población y hacer estimaciones de algunos parámetros de su ciclo vital.

W.F. Perrin
Southwest Fisheries Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, California 92038, USA

T.D. Smith
Southwest Fisheries Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, California 92038, USA

G.T. Sakagawa
Southwest Fisheries Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, California 92038, USA

Introduction

Tuna fishermen in the eastern tropical Pacific kill dolphins incidentally in the course of their seining operations (Perrin, 1969; NOAA, 1972). About 3 years ago, we set out to assess the impact of this on the dolphin populations.

This report is a very brief summary of portions of a draft report entitled "The porpoise-tuna problem: review of research progress" (draft title), which was written at this laboratory in August-September 1974, and was made available to the public by the National Marine Fisheries Service (NMFS) in October 1974. There have since been adjustments and corrections to the material in that report, mainly because we were working with preliminary 1974 estimates that changed as the year progressed. Details of the data and analyses referred to in this paper are in the draft report. Revised 1976 estimates of 1974 figures have been used in the relevant sections and were derived from NOAA (1975).[1]

Methods

GENERAL APPROACH

Our chief goal in assessing the impact of the fishery was to establish whether or not the populations are declining. We have done this by comparing estimated exploitation rate (number incidentally killed ÷ population size) with capacity for increase (in simplistic terms, birth rate minus natural death rate). The inputs into these 2 basic parameters are laid out in the flow diagram (Fig. 1). Incidental kill was estimated from the landings of yellowfin tuna from dolphin schools, the number of net sets, and an estimate of average kill per set. Population size was estimated from density estimates extrapolated to known range. Capacity for increase was calculated from estimates of reproductive parameters in the exploited eastern Pacific population and of natural mortality rates in the relatively unexploited western Pacific population.

Two forms of *Stenella attenuata* and 3 of *S. longirostris* exist in the eastern Pacific. The distributions and bases for separation of these forms and their relative importances in the fishery have been described previously (Perrin, 1975). We have concentrated on assessing the status of the most important form, the offshore spotted dolphin (Table 1). We also gave major attention to the eastern spinner dolphin, but have so far only estimated the exploitation rate and not the capacity for increase. For the third major form, the whitebelly spinner, we have thus far estimated only the incidental kill.

MAJOR SOURCES OF DATA

Our major sources of data were the Inter-American Tropical Tuna Commission (I-ATTC), an aerial survey, and the Tunaboat Observer Program.

I-ATTC

The I-ATTC provided data on numbers of purse seine sets on dolphin schools, by vessel class, for the U.S. fleet, and on landings of tuna caught with dolphins by all nations.

Aerial Survey

An aerial survey conducted in January-February 1974 provided data on density of dolphin schools in the eastern tropical Pacific. Approximately 12 000 track miles were flown

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[1] Since this report was written (1974) and revised (1976) a report of further assessments of status of *Stenella* stocks in the eastern tropical Pacific has been issued: Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Pacific Yellowfin Tuna Fishery. Southwest Fisheries Center, Admin. Rep. LJ-76-29, La Jolla, CA, Sept. 1976.

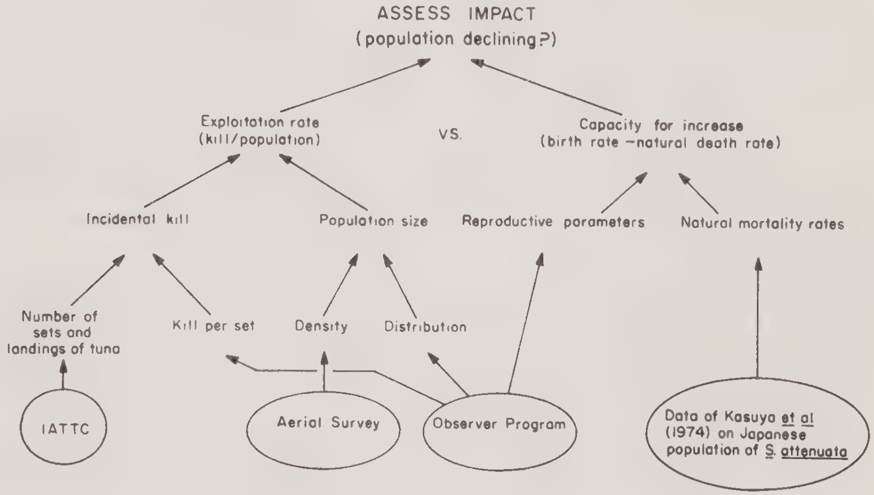
ASSESS IMPACT
(population declining?)
Exploitation rate
(kill/population)
VS.
Capacity for increase
(birth rate – natural death rate)
Incidental kill
Population size
Reproductive parameters
Natural mortality rates
Number of sets and landings of tuna
Kill per set
Density
Distribution
IATTC
Aerial Survey
Observer Program
Data of Kasuya et al (1974) on Japanese population of S. attenuata

FIG. 1. – Flow diagram for assessing impact of incidental fishing mortality on dolphin populations. Major data sources circled.

in a specially modified Gruman Goose, at an average altitude of about 1 500 ft (Fig. 2). Two observers scanned ahead and to the side. The track lines were selected before the survey, independently of any knowledge of the density of dolphin schools. Range capabilities of the aircraft and locations of suitable airports constrained the choice of track lines.

Observer Program

We have had observers on purse seiners every year since 1971. The observers have collected data on numbers of dolphins killed, on their distribution, and on the sex, age and reproductive condition of a sample of the animals killed. We had observers on 5 cruises in 1971, 12 in 1972, 23 in 1973, and about 40 in 1974. We have also collected data during several cruises chartered to NMFS for gear research.

ESTIMATING INCIDENTAL KILL

Our approach in estimating the incidental kill was to extrapolate from estimates of kill per net set in our observer sample to the entire fishery, based on data from the I-ATTC (Fig. 3). We were faced with several problems in this approach:

- the structure of our sample may or may not be representative of the US fleet;
- we did not sample the non-US fleet;
- the Observer Program was effectively limited to the Commission Yellowfin Regulatory Area (CYRA) (Fig. 4) and did not sample the “outside the line” area to the west where roughly 1/3 of the tuna caught with dolphins is taken.

Adjusting for structure of the observer sample

In looking at our earlier data, we found that dolphin kill per net set is correlated with characteristics of the vessel, mainly size. Beginning in 1974 the tunaboats have been required by law to carry observers when requested, so we have been able since then to design our sample to have about the same

Table 1. Populations of spotted and spinner dolphins in the eastern Pacific, and scope of analyses reported in this working paper

Population	Involvement in fishery[1]			Assessment of status[2]				
				Exploitation rate		Capacity for increase		
	Major	Minor?	Negligible	Incidental kill	Population size	Reproductive parameters	Natural mortality	Impact assessed
Coastal spotted dolphin (*S. attenuata* subspecies)		X						
Offshore spotted dolphin (*S. attenuata* subspecies)	X			X	X	X	X	X
Costa Rican spinner dolphin (*S. longirostris* subspecies)			X					
Eastern spinner dolphin (*S. longirostris* subspecies)	X			X	X			X
Whitebelly spinner dolphin (*S. longirostris* subspecies)	X			X				

[1] Major = 1 000 killed incidentally; minor = 100s killed; negligible = 10s or fewer killed.
[2] X = estimates made in present study.

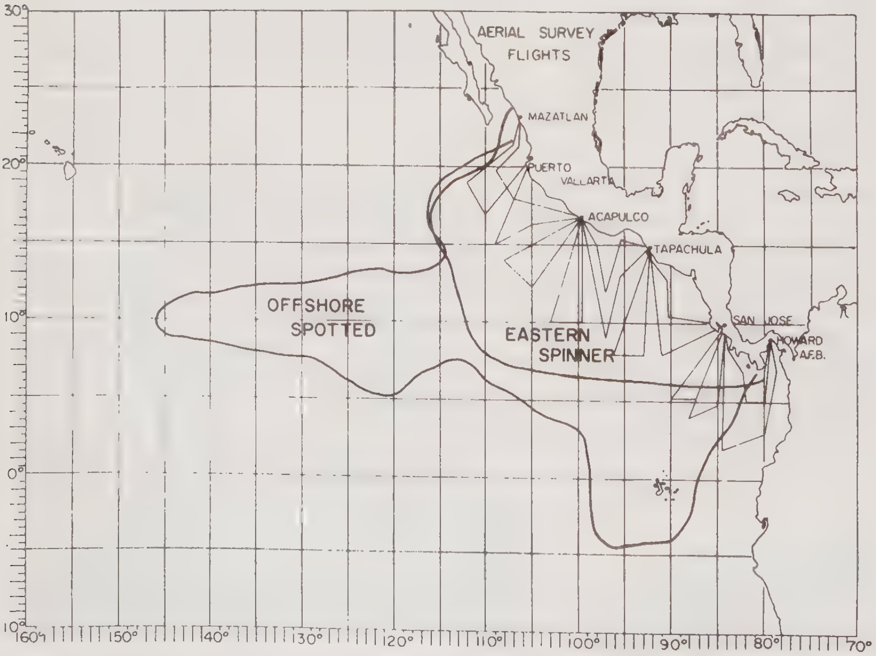
AERIAL SURVEY FLIGHTS
MAZATLAN
PUERTO VALLARTA
ACAPULCO
TAPACHULA
SAN JOSE
HOWARD A.F.B.
OFFSHORE SPOTTED
EASTERN SPINNER
30°
20°
10°
0°
10°
160°
150°
140°
130°
120°
110°
100°
90°
80°
70°

FIG. 2. – Location of track lines on the aerial survey in early 1974. Historical ranges of offshore spotted dolphin and eastern spinner dolphin from Perrin (1974).

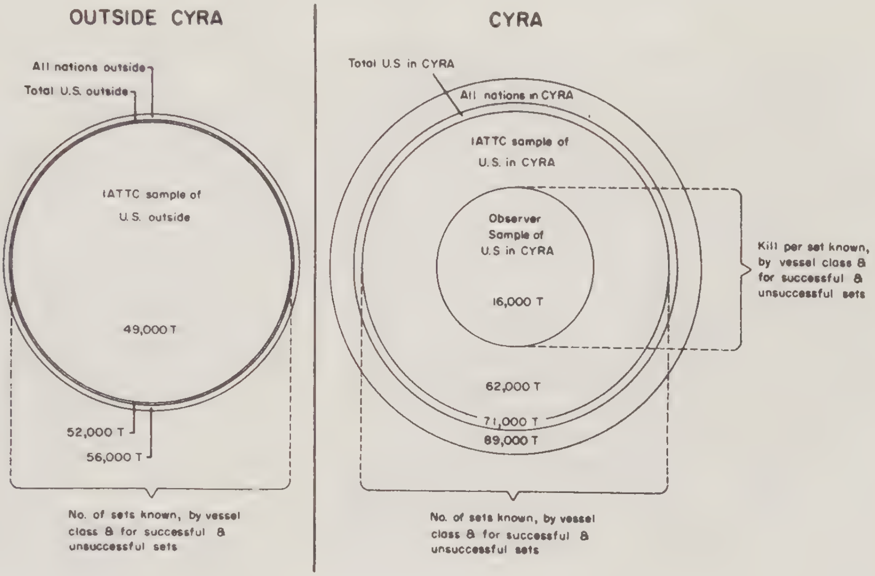
OUTSIDE CYRA
All nations outside
Total U.S. outside
IATTC sample of U.S. outside
49,000 T
52,000 T
56,000 T
No. of sets known, by vessel class & for successful & unsuccessful sets
CYRA
Total U.S in CYRA
All nations in CYRA
IATTC sample of U.S. in CYRA
Observer Sample of U.S in CYRA
16,000 T
62,000 T
71,000 T
89,000 T
Kill per set known, by vessel class & for successful & unsuccessful sets
No. of sets known, by vessel class & for successful & unsuccessful sets

FIG. 3. – Samples used to estimate incidental kill of dolphins in the yellowfin tuna purse seine fishery in the eastern tropical Pacific. Areas of circles are proportional to landings of yellowfin tuna taken in net sets on dolphin schools in 1973. Landings data from I-ATTC.

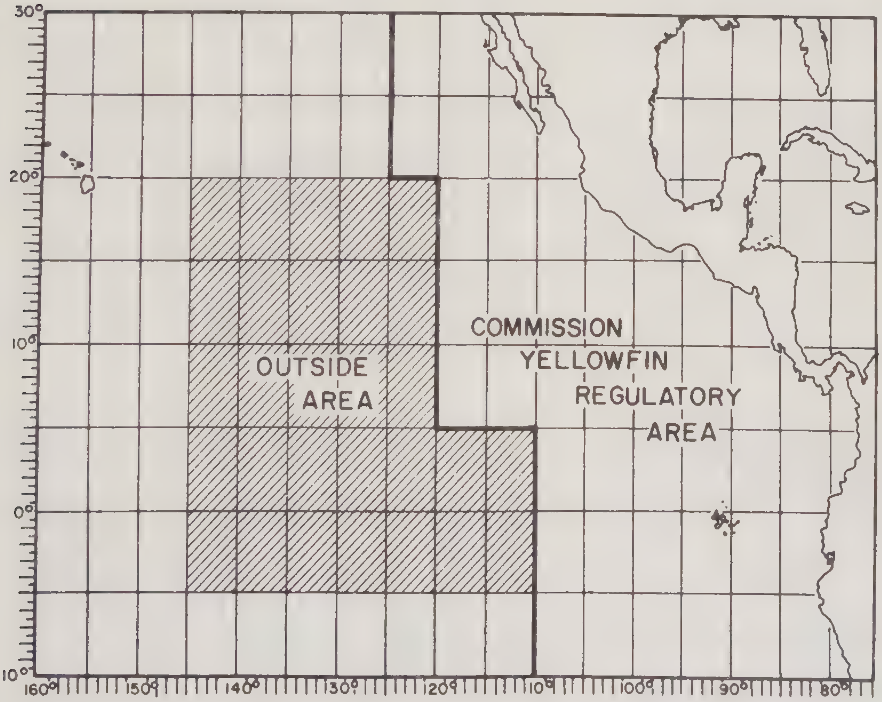
30°
20°
10°
0°
10°
160°
150°
140°
130°
120°
110°
100°
90°
80°
OUTSIDE AREA
COMMISSION YELLOWFIN REGULATORY AREA

FIG. 4. – The major part of the Inter-American Tropical Tuna Commission regulatory area (CYRA) is shown above. Principal zone of "outside" fishing is also indicated.

structure as the fleet in terms of size of vessels. In the earlier years, however, carrying an observer was voluntary, and we know that some of those samples did not well represent the fleet. In 1971, for example, the sample contained proportionately more small, old vessels than did the fleet. Detailed descriptions of the samples and the fleet are in the draft progress report. We attempted to correct for this sample bias by extrapolating on the basis of kill per set for size-age classes of vessels. We used eight strata ranging from 101-200 (short) tons capacity to over 1 200 tons. We also found that dolphin kill is correlated with whether or not the net set is successful in capturing yellowfin tuna, so we stratified our extrapolating procedure also on the basis of success or failure of the set. A successful set was defined as one in which at least 0.025 ton of yellowfin tuna was taken.

Estimating non-US kill

Since we have very few kill-per-set data and no data on sets by vessel class for the non-US fleet, we simply assumed that over-all kill per set is the same as for the US fleet and extrapolated from the US sample on the basis of tons of tuna taken with dolphins.

Estimating kill outside the CYRA

Virtually no observer data were available from outside the CYRA, so we assumed for the purpose of our estimates that kill per set is the same as in the CYRA.

With this approach, we made 4 estimates of incidental kill (of all species):

(1) US kill in the CYRA
(2) kill by all nations in the CYRA
(3) US kill outside the CYRA
(4) kill by all nations outside the CYRA,

using the model

$$\hat{K}_g = \hat{C}_g \left(\sum_{i=1}^{8} \sum_{j=1}^{2} N_{ij}\ k_{ij} \right),$$

where

$\hat{K}_g$ = estimated kill

k_{ij} = kill per set in observer sample stratum ij

N_{ij} = number of net sets in I-ATTC sample of US landings of yellowfin from dolphins

$\hat{C}_g$ = extrapolation factor to account for landings not in I-ATTC sample of US landings

i = vessel size class

j = type of set class (successful or unsuccessful)

g = estimate [(1) to (4) above]

An approximate estimate of variance for $\hat{K}_g$ is

$$\text{var}\,(\hat{K}_g) = C_g^2 [\Sigma\Sigma\, N_{ij}^2\, \text{var}\,(k_{ij})]$$

and the approximate 95 % confidence interval for $\hat{K}_g$ is

$$\hat{K}_g \pm 2\sqrt{\text{var}\,(\hat{K})}.$$

We broke down the total estimates (CYRA + outside) to estimates by species based on the species compositions of samples examined in the Observer Program. The estimates for the spinner dolphin for 1974 were prorated to the eastern and whitebelly populations, based on the ranges of the forms and on the relative percentages of sets in the observer sample known to have been made on each.

ESTIMATING POPULATION SIZE

We estimated the density of schools of the offshore spotted dolphin and eastern spinner dolphin from data collected in the aerial survey. The basic analytical tool used was line transect theory. When a school was sighted, the perpendicular distance from the track line was estimated. The manner in which the number of sightings declined with distance from the track line was used to determine how much area was effectively searched. Four basic conditions must be met in this approach:

(1) schools are distributed at random

(2) transects are placed at random

(3) probability of sighting a school decreases exponentially with distance from the track line, and

(4) probability of seeing a school directly on the track line is 1.0.

Making these assumptions, we estimated density as

$$\hat{D} = (n - 1)/2L\bar{Y},$$

where

n = number of schools sighted,

L = total track miles surveyed, and

$\bar{Y}$ = average perpendicular sighting distance, in this case about 1 mile.

Variance of the density can be estimated as

$$V(D) = \frac{\hat{D}^2}{n}(1 + \frac{n}{n-2} - \frac{n}{DA})$$

We prorated the overall density estimates into estimates for each stock based on the proportion of the total sightings which were of that stock. We also estimated separately for mixed schools because size of single-stock components in mixed schools is different than size of single-stock schools. We estimated separately for pure spotted schools, pure eastern spinner schools, spotted in mixed schools, and eastern spinner in mixed schools.

We then estimated the total number of schools of each stock and school type by extrapolating the density to the known historical range (Perrin, 1975). This makes the assumption that density of schools in the area sampled is representative of the entire historical range. Variance of the estimate of total schools can be calculated as

$$V(\hat{S}_i) = A_i^2 V(\hat{D}_i),$$

where

$\hat{S}_i$ = number of schools or schools components of stock-school type i, and

A_i = area inhabited by schools of stock-school type i

Then, using estimates of average school size (or single-stock component size) from the Observer Program, we estimated the total number of dolphins for each stock-school component type as

$$\hat{N}_i = \hat{C}_i\hat{S}_i,$$

where

$\hat{N}_i$ = total number of dolphins in stock-school type i, and

$\hat{C}_i$ = average size of schools of stock-school type i.

Variance can be calculated as

$$V(\hat{N}_i) = V(\hat{C}_i)S_i^2 + V(\hat{S}_i)\hat{C}_i + V(\hat{C}_i)V(\hat{S}_i).$$

We then added the single-stock school and mixed-stock school components to obtain an estimate for each of the 2 stocks:

$$\hat{P}_j = \Sigma N_{ij}$$

where

$$\hat{P}_j = \text{population of stock j.}$$

The variances of N_i are additive. We expressed the population estimates as interval estimates, which were ± 2 standard deviations from the point estimates. This interval should contain the true value at least 75 % of the time.

We used average school size estimates from the Observer Program, because the sample size from the aerial survey was very small and if used would have greatly increased the variance of the population estimate. This was justified because the aerial estimates did not differ significantly from the Observer Program estimates.

For the 1974 estimates, porpoise-school density estimates from the aerial and ship surveys were made in the aggregate. The ship survey density estimates were also made by stratifying by season and sub-area and computing an average, weighted by the geographical area of each stratum. Additional estimates of density were made which combined the aerial and ship survey. Assuming that the ship survey estimates of density tend to be biased, either due to concentrated fishing for yellowfin tuna associated with dolphins or alternately fishing for yellowfin tuna and other species not associated with dolphins, a correction factor was obtained by the ratio of the aerial survey density to the ship survey density in the period and area of overlap. This ratio was applied to the full range of the ship survey, which is more extensive in areal coverage than the aerial survey. This combined approach additionally assumes that the aerial survey density estimates are accurate and the degree of bias in the ship survey is constant throughout its range.

It is important to note that the estimated population size ranges are ranges of *point* estimates rather than probabilistic confidence intervals. Even though approximate variances were computed for the density and school size estimates and their combination, it is meaningless to try to place a probabilistic confidence interval on the current estimates, because neither the geographical range of each stock is known precisely nor does an estimate of its variance exist. More extensive aerial surveys, ship surveys independent of fishing, or alternate methods will have to be mounted to establish single point estimates with probabilistic confidence bounds.

The major criticisms that can be made of the population estimates are:

- Density of schools may not be the same throughout the ranges. There may be areas of higher or lower density in the unsurveyed offshore parts of the ranges. This could bias the estimates either way.
- The actual range at any time is probably smaller than the historical range. There may be seasonal migrations and year-to-year changes in the range occupied, caused by large-scale environmental fluctuations, e.g. the El Niño condition in 1973. This would bias the estimates upward.
- The assumption that all schools directly on the track line were seen may not be valid. If some schools were missed, this would bias the estimate downward.

ESTIMATING REPRODUCTIVE PARAMETERS

The samples, methods and analyses used in the studies of the life history of *S. attenuata* are described in detail in Perrin, Coe and Zweifel (1976). The studies were based on about 10 000 specimens collected in the Observer Program. The primary inputs into the status assessment are the estimates of age-specific pregnancy rate. We estimated age by looking at growth layers in the teeth. There are 2 sources of uncertainty in the pregnancy rate estimates. One has to do with the number of growth layers deposited yearly in the teeth, and the other concerns the rate of change of pregnancy rate with age. We could not satisfactorily resolve either of these uncertainties, so the inputs into the assessment model were in terms of alternatives, i.e., 1 layer or 2 tooth layers accumulated yearly in adults, and pregnancy rate being either constant, decreasing "slowly", or decreasing "rapidly" with age (defined below).

ESTIMATING CAPACITY FOR INCREASE

The capacity for increase is basically the difference between the gross annual production and the average annual natural mortality. It changes when the environment or the size of a population changes. It is to be expected that capacity for increase increases when a population is exploited.

The basic approach used to estimate capacity for increase is based on Leslie matrix models. The basic inputs are age-specific pregnancy rates and age-specific natural mortality rates. These rates are combined in a matrix which can be used to project the population forward in time and to determine the capacity for increase implied by the naturality and mortality rates. The model equation of interest here is:

$$\underline{M}\,\vec{N} = \lambda\,\vec{N},$$

where

$\underline{M}$ is the Leslie matrix describing the western Pacific stock,

$\vec{N}$ is the age structure vector, and

λ (lambda) is a scalar constant indicating the annual change in the population size with the life history parameters incorporated in the Leslie matrix $\underline{M}$.

If λ is equal to 1.0, the population neither increases nor decreases in size. If it is less than or greater than 1.0, the population decreases or increases, respectively. The capacity for increase is defined as $(\lambda - 1)/\lambda$.

We do not have estimates of natural mortality rates from the fishery because we cannot separate natural mortality from incidental mortality. Biological data are available for an unexploited spotted dolphin population near Japan (Kasuya, Miyazaki and Dawbin, 1974). These data can be used to derive natural mortality rates to use as first approximations for the rates for the eastern Pacific stock. Kasuya, Miyazaki and Dawbin (1974) did not give estimates of the mortality rates of immature animals more than 1 year old. They did give estimates for the mortality rate of first-year calves. These estimates are very low and are not consonant with an equilibrium population, given the calving intervals, which are more directly calculated and seem reasonable.

Therefore, we estimated new mortality rates for calves and rates for older immature animals indirectly. If the adult mortality rates and the reproductive rates estimated for this stock hold, and if the population is in equilibrium, certain values of mortality rates for calves and older immature spotted porpoise are implied. These implied values are determined as those which satisfy the model equation when $\lambda = 1.0$.

We then determined the capacity for increase for the eastern Pacific stock by combining in one matrix the mortality schedule estimated for the western Pacific stock and the reproductive schedule estimated for the eastern Pacific stock. Analysis of this model yielded the desired estimates of capacity for increase. A basic assumption is that the reproductive rates have increased in the eastern Pacific stock due to a decrease in stock size, while the natural mortality rates have not changed.

These estimates of capacity for increase can be directly compared to the annual incidental exploitation rate determined as the ratio of the estimate of numbers killed to the estimated population size. If the incidental exploitation rate is less than the capacity for increase, the population should increase; and if it is greater than the capacity for increase, the population should decrease.

It should be noted that this analysis assumed that the incidental mortality occurs equally over all age classes. It also assumes that the population age structure has had time to achieve a stable form. Both of these assumptions, especially the latter, need to be examined further.

Results

OFFSHORE SPOTTED DOLPHIN

Incidental kill

The estimated incidental kill as declined each year since 1972 (Table 2) to about 72 000 in 1974, of which about 75 % is ascribable to the US fleet.

We stress the fact that these estimates must be considered minimal estimates for several reasons, to wit.

- Only animals known to be dead were counted; we have made no attempt to take into account the injured animals, some of which can be presumed to have died after release from the net.
- Kill data were gathered only from US vessels, which probably perform better in preventing incidental mortality than do most non-US seiners. The non-US fleets contain many small, old vessels that were formerly in the US fleet.
- Some observer effect can be presumed. With the stratified approach, the problem of representation of the fleet in terms of vessel characteristics is solved, but kill rates may be higher on cruises not accompanied by observers than on cruises with observers.

Population size

We saw 54 schools containing offshore spotted dolphins along the 12 000 track miles of the aerial survey. The aerial and ship survey density estimates, along with the geographical ranges and average school sizes resulted in the following total range in estimated population size:

Stock	Estimated total range of population size (millions of animals)
Offshore spotted dolphin	2.8-4.2

The lowest values of the total range result from using the early-season density averages of the combined aerial and ship surveys. The highest values of the total ranges result from using the early-season density averages of the ship survey alone.

The estimated total ranges in population size can be centralized further, because certain of the density estimates are preferred over others. The ship survey is preferred over the aerial survey because of its broader areal coverage. The all-season density averages are preferred over the early-season density averages because of the biases discussed above. The sub-area density averages are preferred over the aggregate density averages because of apparent differences in density among subareas. Combining these preferences results in the following centralized ranges in estimated population sizes:

Stock	Estimated centralized range of population size (millions of animals)
Offshore spotted dolphin	3.1-3.5

The lowest values of the ranges result from the combined aerial and ship surveys and the highest result from the ship survey alone. We have no basis to choose between them.

Capacity for increase

The estimate of capacity for increase depends on the choice of alternative assumptions about life history. For tooth layering, the basic options are 1 or 2 layers per year. For reproduction, the basic options are the frequency of reproduction after sexual maturity being constant with age or declining with age. Consideration of all the reasonable alternatives results in a range of estimates of capacity for increase of –2.5 % to +6.6 % per year as shown in Table 3.

None of the alternatives shown in Table 3 can be eliminated with certainty. However, there is some basis for choice. One tooth layer deposited per year has been suggested for the western Pacific population of *S. attenuata* by Kasuya, Miyazaki and Dawbin (1974). One layer per year has also been suggested for other closely related delphinids, including *S. coeruleoalba* (Kasuya, 1972) and *Tursiops truncatus* (Sergeant, Caldwell and Caldwell, 1973). Two tooth layers have been suggested for *Delphinapterus leucas* (Sergeant, 1973), but this form is less closely related to *Stenella*. Thus, it is reasonable to assume the tooth layering for the spotted dolphin is basically 1 per year.

The estimates of frequency of reproduction with age are based on the relationship between pregnancy rates and numbers of tooth layers. The observed data suggest a decrease in pregnancy rate from 0.6 at 7 layers to 0.4 at 12 layers (Perrin, Coe and Zweifel, 1976). This is termed "decreasing rapidly" in Table 3. The determination of numbers of layers is difficult after the pulp cavity closes at about 12 layers. If the pregnancy rate observed for 12-layer animals is actually the pregnancy rate for all animals age 12 layers or older, then pregnancy rate declines more slowly with age. This is termed "decreasing slowly" in Table 3. Because of the difficulty in reading layers for older animals, it is most reasonable to assume that the reproduction rate either declines slowly with age or is constant with age.

Assuming 1 tooth layer per year and either constant, or slowly decreasing, reproductive rates with age, one obtains a range of estimates of capacity for increase of 1.4-4.0 % (Table 3). Although the other hypotheses cannot be completely ruled out and must be allowed as possibilities, this range represents the most likely values, given present information.

Table 2. Estimated incidental kills of spotted and spinner dolphins in the eastern tropical Pacific, 1971-74, in thousands

Year	Spotted dolphin [1]			Spinner dolphin		
	US	Non-US	Total	US	Non-US	Total
1971	179.7	4.6	184.3	126.4	3.2	129.6
1972	237.6	32.7	270.3	56.7	7.8	64.5
1973	90.6	17.1	107.7	56.9	10.7	67.6
1974			72.0			36.0
						21.0 (eastern)
						15.0 (whitebelly)

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[1] Estimates are for 2 populations: (1) coastal spotted and (2) offshore spotted. All of this kill is assigned to the offshore spotted dolphin population, although some coastal spotted dolphin are involved.

Table 3. Possible capacity for increase for *Stenella attenuata* as percent of current population size under alternative assumptions

Reproductive rate with age	Numbers of tooth layers per year	
	One	Two
Constant	2.3 - 4.0	2.9 - 6.6
Decreasing		
Rapidly	– 1.0 - + 0.3	– 2.5 - – 0.8
Slowly	1.4 - 2.6	1.8 - 3.3

Impact of the fishery

The estimate of impact is based on the revised estimates of kill and population size, using 2 approaches to estimating sustainable yield.

Perrin, Coe and Zweifel (1976) estimated that the rate of gross annual production of calves is about 14.4 % of the offshore spotted dolphin population in the eastern Pacific. This estimate is predicted upon their assumption that the samples are representative of the actual population. Perrin, Holts and Miller (1975) estimated the gross annual production rate of calves for spotted dolphin of the western Pacific to be about 8.7 % from data presented by Kasuya, Miyazaki and Dawbin (1974). The western Pacific population is thought to be very lightly exploited and may be in equilibrium; the adult female annual natural mortality rate was estimated to be 7.4 % (Kasuya, Miyazaki and Dawbin, 1974) but juvenile and male mortality rates are probably higher, so the population's average natural mortality rate is probably near the gross annual production rate of calves. Perrin, Coe and Zweifel (1976) suggest that the higher reproductive rate in the eastern Pacific population might be a population response to exploitation, because the individual reproductive parameters differ between the 2 populations in a manner consistent with that hypothesis. If the hypothesis is true, then the reproductive rate of the western Pacific spotted dolphin, 8.7 %, is an estimate of the natural mortality rate, and carrying out the analogy with a simple model indicates that the present eastern Pacific population might sustain an annual incidental fishing mortality rate of 4.4 % or more, if the natural mortality rate were concomitantly depressed. Using this estimate is an alternative to the approach taken in calculating the preliminary estimates, where an age-specific model was used.

The total mortality of offshore spotted dolphins in the eastern Pacific during 1974 is estimated to be 72 000 animals. The central estimates of population size are 3.1-3.5 million animals, with a total range of 2.8-4.2 million animals, giving a central range for the 1974 incidental fishing mortality rate of 2.1-2.3 % and a total range of 1.7-2.6 %. The estimates of the incidental fishing mortality rate are below that indicated as sustainable in the simple model, 4.4 % indicating that the population would increase but at a slow rate of 1.7 % per year or slightly more. The estimates of the incidental fishing mortality rate are within the probably range of that indicated as sustainable in the age-specific model, indicating that if the population were changing it would be doing so at a very low rate (i.e., between decreasing at 1.2 % and increasing at 2.2 % per year). This leads to the tentative conclusion that if the offshore spotted population were changing under the 1974 level of incidental fishing mortality, it was probably doing so at a low rate.

We have done some back extrapolations

on the basis of earlier fishing activity and kill rates to examine the question of whether or not the population is at its original size. The balance of evidence suggests that there has been a decline. We do not know yet how great it has been. These analyses are still being revised and refined.

EASTERN SPINNER DOLPHIN

Incidental kill

The estimated kill of spinner dolphins in 1974 was 36 000, of which 21 000 are estimated to have been eastern spinner dolphins.

Population size

We made 36 sightings of eastern spinner schools on the aerial survey. This extrapolates to a population of 1.0-1.5 million animals, which can be centralized as described for the spotted dolphin, to give a range of 1.1-1.2 million.

Impact of the fishery

Estimates of some life history parameters are available (Perrin, Holts and Miller, 1975). Gross annual reproductive rate was estimated to be 6.4 % for 1973 and 9.8 % for 1974, with a pooled estimate of 8.3 %. This is considerably below the rate estimated for offshore spotted dolphins in the eastern Pacific, suggesting that the stock of the eastern spinner dolphins cannot bear as much *total* mortality as the stock of spotted dolphins. However, depending on the natural mortality rate, it might sustain a higher or lower incidental fishing mortality rate than that of the offshore spotted dolphin. The relatively high rate of reproduction exhibited by the spotted dolphin may be a response to exploitation, as suggested by Perrin, Coe and Zweifel (1976) and Perrin, Holts and Miller (1975). It is possible that spinner dolphins have been less heavily exploited than spotted dolphins in the past (e.g., prior to 1971); comparisons of several biological parameters with other cetaceans support this contention (Perrin, Holts and Miller, 1975).

In 1974, the estimated central range of population size point estimates of eastern spinner dolphins was 1.1-1.2 million animals, with a total range of 1.0-1.5 million animals. The kill of eastern spinner dolphins in 1974 was estimated to be 21 000 animals. Thus the estimated central range of the annual rate of mortality caused by fishing was 1.8-1.9 %, with a total range of 1.4-2.1 %, which is not appreciably different from that for the offshore spotted dolphin. This, and the apparent absence of populational response to exploitation lead, as for the offshore spotted dolphin, to the tentative conclusion that if the eastern spinner dolphin population was changing in 1974, either increasing or decreasing, it was doing so at a low rate.

WHITEBELLY SPINNER DOLPHIN

For the whitebelly spinner, we know only that an estimated 15 000 were killed. We, as yet, have no estimates of population size or capacity for increase.

Discussion

SHORTCOMINGS OF THE STUDIES

We have established that the aerial survey approach is feasible, but our population estimates are weak because they involve extrapolation to large portions of the ranges that were not surveyed. Also, the estimates based on aerial surveys have high variability due to small sample size. We need an estimate for the whitebelly spinner population. We have not yet surveyed on a large enough scale.

The problem of calibration of growth zones in the teeth remains. Until this is settled, the estimates of reproductive parameters are only provisional. We do not, of course, have any estimates yet for the spinner dolphins.

The estimates of measured incidental kill may be inaccurate because of the lack of data for the area outside the CYRA and for the non-US fleet. We also need to estimate the now unmeasured kill.

RECOMMENDATIONS FOR RESEARCH

In order to assess the status of the stocks adequately there is a need to:

- Monitor the sizes of all dolphin stocks involved in the tuna fishery, using expanded surveys that adequately cover the geographical range of each stock. Population estimates should be made over a period of years, so that the existence or absence of trends can be firmly established. Additional sources of potential information, such as I-ATTC data, need to be explored to assist in establishing the history of the status of the stocks.
- Continue to monitor the incidental kill of dolphins in the tuna fishery, through a continued Observer Program or some other scheme. Kill should be estimated stock by stock. An attempt should be made to measure possible effects on dolphins stocks in addition to the presently measured direct incidental mortality.
- Estimate the life history parameters for the several spinner and whitebelly dolphin stocks and resolve the question of toothlayer deposition rate in the spotted dolphin, which is central to estimating parameters.

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APPROACHES TO RESOURCE ASSESSMENT FOR LOBSTER, BOTTOM FISH, MONK SEAL, AND GREEN TURTLE STOCKS IN THE NORTHWESTERN HAWAIIAN ISLANDS

by

Jeffrey J. Polovina, Stephen Ralston and Jerry A. Wetherall
Southwest Fisheries Center, Honolulu Laboratory
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
Honolulu, Hawaii

1. INTRODUCTION

The Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service (NMFS), is assessing the stocks of spiny lobster, *Panulirus marginatus*, a snapper (Lutjanidae) and grouper (Serranidae) complex of bottom fishes, the Hawaiian monk seal, *Monachus schauinslandi*, and the green turtle, *Chelonia mydas*, in the Northwestern Hawaiian Islands (NWHI).

The NWHI is an area of reefs, banks and islands located northwest of Honolulu stretching from Nihoa Island 1 250 n mi northwest to Kure Atoll. The spiny lobster and bottom fish resources support a modest fishery in the NWHI. The monk seal is an "endangered" species breeding only in the NWHI and the green turtle is considered a "threatened" species under the US Endangered Species Act.

2. SPINY LOBSTER

The spiny lobster fishery began in 1975 when the NOAA ship TOWNSEND CROMWELL, a research ship assigned to the Honolulu Laboratory, documented good catch rates of spiny lobster, at the lower end of the chain. In 1975 the commercial catch was 2 000 kg. Each subsequent year the catch has increased and the current catch for 1981 is estimated at 300 000 kg (Skillman and Ito, 1981). The rapid development of this fishery has raised concern that overfishing may occur and work to develop a fishery management plan (FMP) was initiated by the Western Pacific Regional Fishery Management Council. The Honolulu Laboratory has contributed to this FMP by undertaking work to: 1) Determine the distribution of the resource throughout the NWHI chain, and 2) estimate the sustainable yield of the resource. The data available for these analyses consist of sampling data collected on research cruises of the TONWSEND CROMWELL, and some commercial catch and effort data.

The data collected by the TOWNSEND CROMWELL represent a systematic sampling survey with catch and effort data collected from 0.1° squares around the banks and islands of the NWHI. This catch-per-unit-effort (cpue) data were used to prepare charts of the relative abundance of the spiny lobster stock throughout the NWHI (Uchida *et al.*, 1980).

The estimation of sustainable yield for the region was based on the commercial catch and effort data base. There currently is no regulation that requires commercial vessels to report their catch and effort and, hence, only an intermittent catch and effort data series submitted on a voluntary basis was available. While the catch and effort time series were too short and sporadic for surplus production analyses, a series of catch and effort data which represented intensive trapping applied to a previously unexploited population was available for analysis. Based on this intensive catch and effort data, an estimate of pre-exploitation population size (N_0)and catchability (q) could be obtained by computing a regression of cpue on cumulative catch (Leslie method, Ricker 1975, p. 150).

Another approach to estimate pre-exploitation biomass was applied to data collected from Necker Island at the lower end of the chain where much of the earlier commercial effort was directed. This approach was based on a method proposed by Allen (1966) in which population size and catchability are estimated in a manner which minimizes the sum of squares between the actual catch and the predicted catch, given effort. In its most general form, this model assumes that the rate of natural mortality is constant while recruitement may vary over time. This most general form requires that the user supplies estimates of the natural mortality and recruitement rates. We did not have any estimate of recruitement rate and hence modified Allen's model. We assumed that the ratio of the rate of natural mortality to the recruitement rate was constant over the two-year period for which data were available. This ratio together with population size and catchability are then estimated by least squares. Application of this method to 24 months of commercial catch and effort data from Necker Island produced estimates of catchability and population size which were in agreement with the estimates obtained from the same site by an intensive fishing analysis (Polovina and Tagami, 1980).

Once pre-exploitation population size, and hence biomass, were obtained for several areas where research sampling cpue data were available, a linear regression of biomass per unit area on research sampling cpue was used to obtain an estimate of total biomass for the entire NWHI. Based on this total estimate of pre-exploitation biomass (B_o), rough approximation of lobster maximum sustainable yield (MSY) for the NWHI were obtained based on Gulland's (1971) relationship:

$$MSY = M\ B_o/2$$

where M = annual instantaneous natural mortality,

and a method proposed by Pauly (1981):

$$MSY = 2.3\ \bar{w}^{-0.26}\ B_o$$

where $\bar{w}$ is defined as the average of the weight at first maturity and the maximum weight of the lobster in the population (in grams).

To estimate natural mortality (M) for Gulland's relationship, the following relationship (Beverton and Holt 1956) was used on data obtained at sites with little or no fishing:

$$F+M = K(L - \bar{L})/(\bar{L} - L_{min})$$

where $\bar{L}$ is the mean carapace length from the trappable population, L_{min} is the minimum carapace length from the trappable population, and K and L are the parameters from the von Bertalanffy growth equation which were estimated from modal analysis of length-frequency data.

While these methods produced estimates which can only represent rough approximations, it appears that the results nonetheless represent reasonable first approximations. The approach described produced estimates of annual MSY ranging from 100 000 kg to 200 000 kg (WPRFMC, 1981). The yield for 1981 was 300 000 kg; however, the substantial decline in catch rate and lobster size suggests that this yield is not sustainable. Once the FMP is in force and commercial catch and effort data can be collected, it is anticipated that these estimates will be revised.

Two difficulties encountered in this analysis were the availability of only short and sporadic commercial catch and effort data and the difficulty of obtaining precise estimates of growth parameters. Both tagging data and analysis of modes and modal progressions of length-frequency data were used to estimate growth parameters. The tagging approach suffered from insufficient recoveries and relatively slow apparent growth for the animals recovered possibly due to an effect of tagging on growth. The analysis of length-frequency data showed large variances in growth due to the difficulty in identifying modes which was apparently caused by the large variance in size among lobsters of the same cohort.

3. BOTTOM FISHES

The bottom fish fishery exploits a complex of species, especially snappers (Pristipomoides spp., Etelis spp., and Aprion virescens), but including also jacks (Carangidae: Caranx spp., Carangoides spp., and Seriola dumerili) and a grouper (Ephinephelus quernus). The fishery is conducted in deep (60-340 m) offshore waters using baited hook-and-line gear, and powered mechanical line-haulers.

Bottom fishes have been exploited around both the main Hawaiian Islands and the NWHI since at least 1945. However, until recently only one vessel regularly fished in the NWHI. Recently more commercial vessels have begun exploiting bottom fish stocks in the NWHI, but the data base of commercial catch and effort for the NWHI is not sufficient to perform a stock-production analysis. A larger data base for comercial catch and effort data around the main Hawaiian Islands is available and a stock-production analysis of the bottom fish resource around the main islands of the State was completed using a 20-year series of catch data collected by the Hawaii Division of Aquatic Resources (Ralston and Polovina, in press). Although fishing effort statistics were not specifically maintained, a computer program sorted through the data base and tallied the number of fisherman-days expended each year in the fishery. The stock was treated as a multispecies fishery and analysed by application of the Total Biomass Schaefer Model (TBSM) (Pope, 1979). Cluster analysis of the data showed that bottom fish species could conveniently be divided into three somewhat distinct groups which appeared to be segregated on the basis of depth and could be analysed by the use of TBSM. Using aggregation theory it was demonstrated that the cluster groups provided a more accurate and biologically meaningful way of expressing production in a multispecies framework. The analysis also showed that the fishery is currently close to MSY.

The chief liability of this study was that the measure of fishing effort which was employed had to be determined after the fact. Interpretation of the statistic used became most difficult as a result. Furthermore, the recreational catch of bottom fish in Hawaii is unreported and thus unaccounted for. Consequently, estimates of surplus production from this analysis can only be considered as a lower bound for yield potential.

A yield-per-recruit analysis of Pristipomoides filamentosus has also been completed. This is the most important species in the fishery and it was studied in some depth to complement the results of the stock-production study. In an investigation of the growth dynamics of this species, the density of daily increments in sagittal otoliths was integrated to estimate age (Ralston and Miyamoto in press). The daily periodicity of the increments was validated by in vivo tetracycline labelling of otoliths and examination of shifts in field-sampled size-frequency distribution. An age-length key was generated from regression statistics derived from the estimated age-length data. This key was then applied to length-frequency samples to estimate mortality rate using the catch-curve method. Experimental fishing trials were conducted to assess the likelihood of severe size bias in these hook-and-line samples. The yield-per-recruit calculations for P. filamentosus showed that eumetric conditions currently prevail for this species at a relatively high level of yield (Ralston, 1981). This result is considered compatible with the finding that the fishery is now operating close to its MSY.

A major difficulty in these studies was the labor-intensive nature of working with daily increments in otoliths. In this regard, the growth of P. filamentosus remains the topic of ongoing study, as is the growth of other bottom fish species. Furthermore, more extensive length-frequency samples of these fishes would have been desirable.

The results of these stock assessments have shown that the bottom fish resources of the main Hawaiian Island are currently being intensively exploited and yet further expansion of the fishery into the NWHI appears feasible on biological grounds. Ancillary studies concerning the diets and fecundities of selected bottom fish species are also currently being pursued (Uchida, Ito and Uchiyama, 1979), and these should assist in the management of bottom fish stocks.

4. HAWAIIAN MONK SEAL AND GREEN TURTLE

Both the Hawaiian monk seal and the green turtle are protected under provisions of the US Endangered Species Act. Assessing the status of their populations for stock protection and rehabilitation is therefore a major goal of the Honolulu Laboratory.

The programme for assessment of green turtles is in its second year. The long-range objectives are to gather information on reproductive ecology, migratory patterns, growth rates, mortality rates, and other life history characteristics which will lead to an understanding of turtle population dynamics. Mark-and-recapture techniques will be used extensively. Metal flipper tags have been applied by non-NMFS biologists to over 1 100 turtles since 1973, but mostly to adult animals in the NWHI. In 1981 NMFS scientists experimented with tagging of green turtle hatchlings using auto-transplanted tissue plugs. Results were very promising, so in 1982 the Honolulu Laboratory will mark several hundred hatchlings with reversed scute plugs as they leave their nests at French Frigate Shoals.

Honolulu Laboratory research on the Hawaiian monk seal is also in its second year. Past work has been carried on by sientists from the Department of the Interior, the Department of Commerce, and by researchers on contract to the Honolulu Laboratory and to the Marine Mammal Commission.

Part of the 1981 programme involved the development and implementation of a recovery plan for the monk seal population, and this included an outline of research needs for stock assessment and an understanding of seal population dynamics. A variety of assessment techniques might be employed, including aerial and ground counts to develop abundance indices and mark-and-recapture methods using natural marks, bleach marks, or tags.

During 1982 a pilot tagging project at Lisianski Island will be undertaken to test the suitability of plastic cattle tags applied to the hind flippers of about 15 weaned monk seal pups. The tagged pups will also be bleach marked, as will an equal number of untagged pups. Data will be collected on temporal and spatial aspects of haul-out behavior, inter- and intra-specific interactions, and on other aspects of their early life history. If the effects of the tagging procedure and the presence of the tags are judged to be insignificant, a pup-tagging programme throughout the breeding range of the Hawaiian monk seal will be proposed for 1983.

Tags may also be applied to adult seals in future research. The tagging studies will produce critical information on age- and sex-specific mortality rates, age at first reproduction, reproduction rates, inter-island movement, and population size.

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Influence of Hook Size in the Hawaiian Deep-sea Handline Fishery

STEPHEN RALSTON[1]

Fisheries Research Institute, College of Fisheries, University of Washington, Seattle, WA 98195, USA

RALSTON, S. 1982. Influence of hook size in the Hawaiian deep-sea handline fishery. Can. J. Fish. Aquat. Sci. 39: 1297 – 1302.

Experimental bottom fishing trials were conducted in the Northwestern Hawaiian Islands where four different hook sizes (Nos. 28, 30, 34, and 38) were fished simultaneously. Within this series the biggest hook is about 71% larger than the smallest hook. Alterations in gear within this range have no substantive effect on the catch of bottom fish. In all cases examined, variation in catch statistics associated with differing replications (days and sites) greatly exceeded any effect attributable to different hook sizes. It is concluded that for medium- and large-sized fish, the catch is reasonably representative of those fish which strike the hooks and that a sigmoid selection curve most accurately describes the selective properties of the gear in this fishery.

Key words: gear selection, hook size, bottom fish, replications

RALSTON, S. 1982. Influence of hook size in the Hawaiian deep-sea handline fishery. Can. J. Fish. Aquat. Sci. 39: 1297 – 1302.

Des pêches expérimentales sur le fond ont été pratiquées dans le nord-ouest des îles Hawaii avec quatre grandeurs d'hameçons différentes (n^{os} 28, 30, 34 et 38) utilisées simultanément. L'hameçon le plus gros de la série est environ 71 % plus gros que le plus petit. Entre ces extrêmes, des modifications à l'engin n'ont pas d'effet notable sur les prises de poissons de fond. Dans tous les cas étudiés, la variation des prises dans divers essais se répliquant (quant aux jours et aux sites) dépasse de beaucoup tout effet attribuable à différentes grandeurs d'hameçons. Nous concluons que, dans le cas de poissons de taille moyenne et grande, les prises sont assez représentatives des poissons qui mordent aux hameçons et qu'une courbe de sélection sigmoïde est celle qui décrit avec le plus de précision les propriétés sélectives de l'engin utilisé dans cette pêche.

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MUCH is known of the selective properties of both trawls and gill nets (e.g. ICNAF 1963), and Gulland (1969) describes briefly some methods for evaluating selection by these kinds of gear. In contrast, very little information concerning selection by hook-and-line fishing gear is available. The results of these few studies are somewhat contradictory, and currently it is difficult to generalize concerning the type and extent of bias likely to be present in samples obtained by this method of fishing.

A number of investigators have reported substantial bias in length–frequency samples derived from angling. For example, Fry (1949) found that hook-and-line fishing gear exhibited a dome-shaped selectivity curve for lake trout (*Salvelinus namaycush*), similar to that classically obtained from gill nets. Also, Fraser (1955) reported that smallmouth bass (*Micropterus dolomieui*) are increasingly susceptible to capture by hooks as fish size increases. Both of these authors concluded that size selection by hook and line is relatively severe and strongly dependent upon the size-classes sampled. Similarly, Brock (1962) found that length–frequency distributions of yellowfin tuna (*Thunnus albacares*) summarized from longline catches were quite different from those obtained from the purse-seine and live-bait fisheries. He found that small fish were poorly represented in the former fishery, whereas few large fish were sampled in the latter. Japanese researchers (Koike et al. 1968; Kanda et al. 1978; Koike and Kanda 1978) have suggested that samples of spiny goby (*Acanthogobius flavimanus*), mackerel (*Scomber japonicus*), and pond smelt (*Hypomesus olidus*) collected with hook and line demonstrate a bias towards an optimum catchable length which is in turn dependent upon hook size.

Other researchers have come to somewhat different conclusions. Chatwin (1958) reported that the hook-and-line selectivity curve of lingcod (*Ophiodon elongatus*) is sigmoidal and constant above a certain minimal size, analogous to selection curves obtained from trawl fisheries (Gulland 1969). Both McCracken (1963) and Saetersdal (1963) reported similar findings while studying Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). In addition, these authors found that variation in hook size tended to shift the

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[1] Present address : Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Honolulu, HI 96812, USA.

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minimum size of capture but did not affect the catch of large fish. Moreover, Allen (1963) concluded that samples of New Zealand trout obtained by fly-fishing were unbiased. Similarly, Leclerc and Power (1980) found fly-fishing to be the least selective of three different methods of sampling for brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*).

This study began as an attempt to evaluate the type and extent of size bias present in the catch of bottom fish landed in the Hawaiian deep-sea handline fishery (Hawaii Department of Land and Natural Resources 1979; Ralston 1981; Ralston and Polovina 1982). Because of the conflicting nature of previous work on this topic, it became necessary to investigate the process of gear selection in this particular fishery. A selection curve can be calculated by comparing independent, unbiased samples with hook-and-line catch statistics. At present there are no similar data concerning stocks of bottom fish in Hawaii and it is not possible to calculate selection curves for this fishery. However, by examining the effect of hook size variation on the catch of bottom fish, one can infer much about the selective properties of fishing hooks.

Methods

Fishing trials were conducted during four research cruises to the Northwestern Hawaiian Islands on the 23-m, 109 gross ton R/V *Easy Rider*. This vessel is capable of multiple fishing activities and is typical of the larger, more powerful craft which have recently entered the offshore handline fishery in Hawaii.

The boat was equipped with three deep-sea bottom fishing rigs composed of Charlin hydraulic motors, Pacific King fishing reels, and ~ 400 m of 150-kg test, braided prestretched Dacron line. Standard equipment on each rig included four #34 Tankichi ulua hooks attached to 75-kg test monofilament leaders and a 2-kg welded reinforcement-bar weight.

The effect of variation in hook size on the catch of bottom fish was studied by simultaneous fishing with hooks of different sizes (Fig. 1). Each of the three fishing reels was rigged with one each of the four differently sized hooks (Nos. 28, 30, 34, and 38) to control for line and fisherman effects. To control for a possible position effect, the locations of the four hooks on each line were determined at random. During experimental trials each fishing line was monitored individually. All hooks were baited with equivalent pieces of cut frozen squid and released to the bottom. The fate of each hook was recorded upon retrieval to the surface. When fish were landed the species and the fork length (FL) or total length (TL) in centimetres were noted, as were loss of bait and broken hooks when appropriate.

Data were summarized according to each day of fishing trials ($n = 17$), which individually were treated as experimental replications. Fishing took place at Necker Island, French Frigate Shoals, Maro Reef, and Midway and Kure Atolls during March and October 1979, and November 1980. Catch statistics included the number and size composition of each species landed on the four different sizes of hooks. These data were analyzed as randomized complete blocks in parametric two-way analyses of variance (ANOVA) when samples were sufficiently abundant, although for two species the size composition data were sparse. In these situations the data were pooled across replications and a simple one-way parametric ANOVA was performed (hook size as treatment effect). Similarly, for the same two species the Friedman test, a nonparametric two-way analysis (Tate and Clelland 1957; Conover 1980), was applied to the number of individuals landed per day because the data matrix contained many zeros.

Results

A total of 1110 fish were landed and measured during the four research cruises. The catch was composed mainly of opakapaka (*Pristipomoides filamentosus*), which alone accounted for 50% of the total. This snapper (Lutjanidae), the target species, is usually found in waters 100–200 m deep. Lesser numbers of other species were also taken: the hapuupuu (*Epinephelus quernus*), a grouper (Serranidae), and the pig ulua (*Pseudocaranx dentex*), a jack (Carangidae). These two species comprised 17 and 21%, respectively, of the catch. Analyses of gear selection in each of these three species were conducted independently.

NUMBER OF OPAKAPAKA

Adequate samples of opakapaka were taken on 12 of the 17 possible trial days. The data were square-root transformed ($\sqrt{x}$) because some cell entries were small whole numbers leading to heterogeneous variances. Application of Tukey's test showed no evidence of non-additivity after transformation ($P \simeq 0.20$, Snedecor and Cochran 1967). The ANOVA showed that the four different sizes of hooks did not catch significantly different numbers of opakapaka per day, although the F statistic was only marginally insignificant ($0.10 > P > 0.05$). Based upon examination of the treatment means there was the suggestion that hook size may affect the number of opakapaka caught in a day, the three smaller hooks being more effective. The data were subsequently analyzed as a one-way χ^2 test under the null hypothesis that the total number of opakapaka caught on each of the four different hook sizes, pooled across all replications, should be equal. This analysis is appropriate because all hooks were always fished simultaneously and the experiment was therefore completely randomized, with catch per hook following the multinomial distribution. Furthermore, a two-way χ^2 analysis of the data showed no interaction between replications and hooks in their joint effect on catch per day ($P \simeq 0.80$). The one-way calculation yielded a significant value ($P \simeq 0.03$), however, demonstrating that smaller hooks are more effective than size No. 38 hooks in catching opakapaka.

A highly significant replication effect is evident in these data (ANOVA, $P << 0.005$), implying that the number of opakapaka caught among differing days and sites is highly variable. The total catch, pooled across hooks, ranged from a high of 58 to a low of 3 individual opakapaka landed per day.

SIZE OF OPAKAPAKA

The effect of hook size variation on the size (FL, cm) of

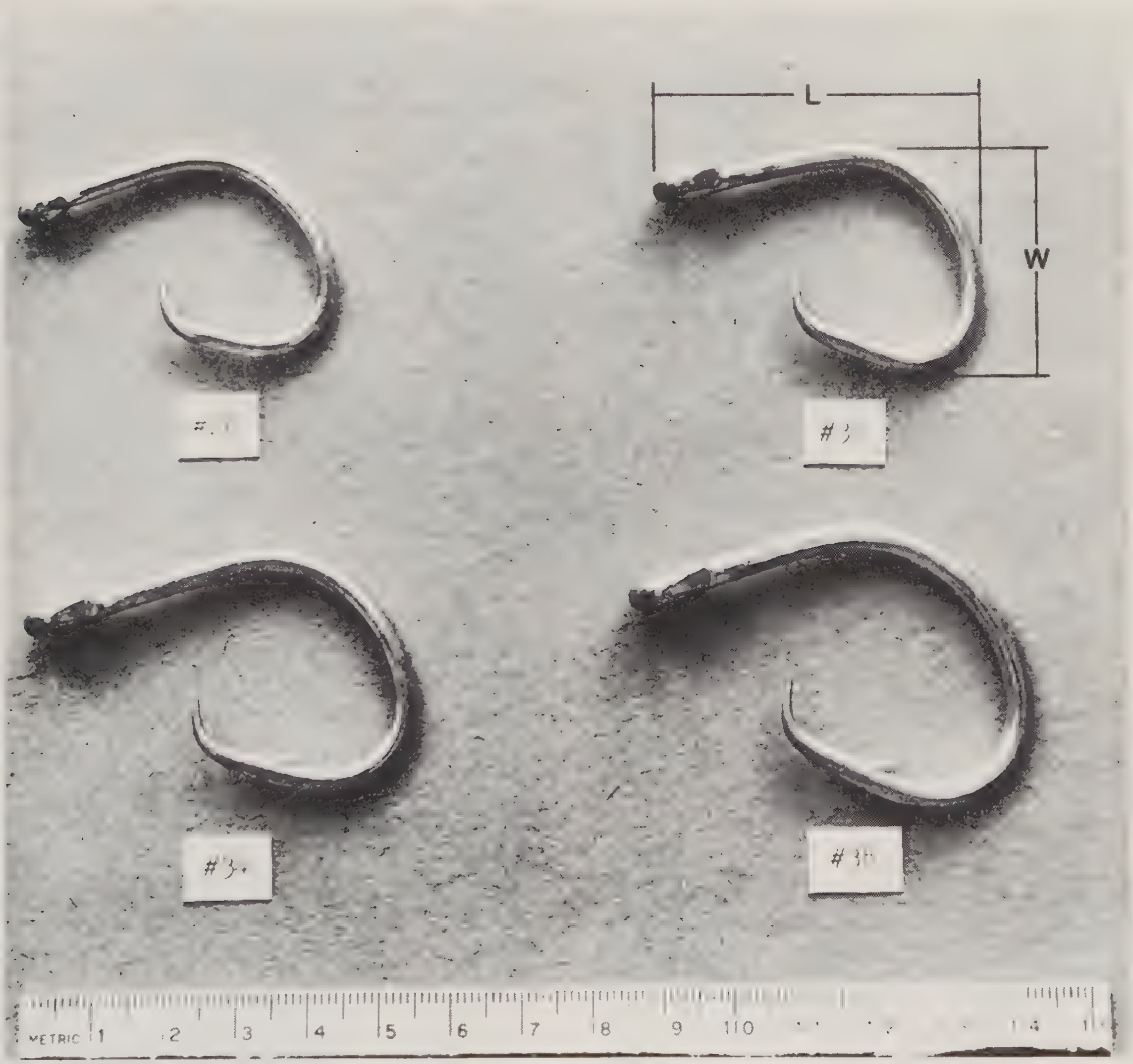

FIG. 1. Four sizes of Tankichi ulua hooks used in experimental fishing trials. The absolute size of a hook was calculated as the product of its length (L) and width (W).

opakapaka landed was examined by means of a two-way ANOVA with repeated observations of unequal sample size (Dixon 1977, program BMDP2V). The analysis was treated as a mixed model with hooks as fixed effects and days as random effects.

Over the size range of hooks tested (Nos. 28–38) there is no indication of a treatment effect. Large hooks appear to be as successful as small ones in catching small fish and vice versa (ANOVA, $P \simeq 0.25$). In comparison, the day of fishing (replication) very strongly affected the size of opakapaka landed ($P << 0.005$). The mean size of opakapaka caught among different days ranged from 37 to 61 cm FL. Most of this variation can be attributed to differences between French Frigate Shoals and Maro Reef in the average size of fish they yield. Furthermore, the analysis suggests that there is no interaction between hook and day effects.

NUMBER OF HAPUUPUU

Sufficient numbers of hapuupuu for analysis were landed on 15 of the 17 possible experimental fishing days. Variable hook size had no discernible effect on the number of hapuupuu landed (Friedman test, $P >> 0.05$) whereas the day fished had a profound effect on this statistic ($P << 0.01$). This is evidenced by the fact that the numbers of hapuupuu caught on the different hooks, pooled across days, ranged from 24 to 35 whereas the numbers caught on different days ranged from 1 to 24. A χ^2 test examining the total numbers of hapuupuu landed, pooled across all replications, was insignificant ($P \simeq 0.55$).

SIZE OF HAPUUPUU

Variation in hook size had no detectable effect on the size of hapuupuu landed, although the F statistic was but marginally insignificant (one-way ANOVA, $P \simeq 0.10$). Because variation attributable to different days of fishing could not be factored out, a more thorough sampling program might demonstrate significant hook effects (larger hooks tending to catch, on average, larger fish).

NUMBER OF PIG ULUA

Sufficient numbers of pig ulua for analysis were taken on 10 of the 17 experimental fishing days. Hook size did not significantly affect the number of pig ulua caught (Friedman test, $0.10 > P > 0.05$). The borderline condition of the test statistic could well be due to sampling error (type I) because no trend was evident in the success of the various hook sizes in capturing this species. Hooks of intermediate size (Nos. 30 and 34) seemed to perform slightly better than the extremes (Nos. 28 and 38). Furthermore, a χ^2 test of the treatment totals, pooled across all replications, showed no difference due to hooks ($P \simeq 0.18$). In contrast, the day of fishing (replications) exerted a strong effect on the numbers landed (Friedman test, $P << 0.01$). The numbers of pig ulua landed on different days ranged from 1 to 47. As with the opakapaka, differences in catch rates of pig ulua between the study sites at French Frigate Shoals and Maro Reef probably account for the preponderance of this effect.

SIZE OF PIG ULUA

All pig ulua data were simply classified according to the size of hook the sample was landed with because the numbers caught were limited. Variation in hook size (Nos. 28−38) had no effect on the size of pig ulua landed (one-way ANOVA, $P >> 0.05$). The mean sizes of fish caught, in ascending order of hook size, were 65.3, 65.1, 65.7, and 65.4 cm FL.

TOTAL NUMBERS OF FISH

To assess whether variation in hook size affects total catch of bottom fish I included the three species already treated, and the incidental catch of kahala (*Seriola dumerili*), ehu (*Etelis carbunculus*), gindai (*Pristipomoides zonatus*), and other species. Catch rate was measured on a daily basis as the mean number of fish caught per drift of the vessel. Drifts generally ranged between 10 and 40 min duration. The computations include all 17 of the experimental fishing days and the analysis performed was a two-way ANOVA.

Variable hook size had no detectable effect on the mean number of fish caught per drift ($P >> 0.10$). In ascending order of hook size, the treatment means for hooks were 0.99, 0.97, 0.92, and 0.86 individuals per hook per drift. Similarly, when the total catch of all species is pooled across all replications, a χ^2 test of the treatment totals is insignificant ($P \simeq 0.22$). In contrast, the day fished (replication) exhibited a strong effect on total catch rate ($P << 0.005$), with replication means ranging from 0.15 to 2.35 individuals per hook per drift. These results indicate that variation in hook size from No. 28 to No. 38 has no appreciable effect on bottom fish catch rate.

TABLE 1. Summary of all analyses performed in assessment of gear selection. Probabilities (P) refer to the chance of obtaining a test statistic under the null hypothesis of no difference due to treatment or replication. N.S. = not significant.

Variable examined	Treatment (hooks)	Replication (d)
Number of opakapaka	$P < 0.05$	$P << 0.005$
Size of opakapaka	N.S.	$P << 0.005$
Number of hapuupuu	N.S.	$P << 0.005$
Size of hapuupuu	$P \simeq 0.10$	—
Number of pig ulua	$0.10 > P > 0.05$	$P << 0.005$
Size of pig ulua	N.S.	—
Total numbers of fish	N.S.	$P << 0.005$
Bait loss	N.S.	$P << 0.005$

BAIT LOSS

The effectiveness of different sizes of hooks at retaining bait provides another means of ascertaining selection. If one hook size loses bait more often than another, it might be concluded that the two hooks draw different samples from the population, assuming strike rate is unaffected by hook size.

Eleven of the 17 possible trial days were used in this analysis, which shows that variation in hook size had no appreciable effect on the mean number of baits lost per drift whereas the day fished had a highly significant effect on this quantity (two-way ANOVA, $P \simeq 0.20$ and $P < 0.005$, respectively). The mean numbers of baits lost per hook per drift among the four hooks, in ascending order of hook size, were 1.65, 1.50, 1.43, and 1.42 whereas among the days fished these figures ranged from 0.82 to 2.11.

Discussion

This simple attempt at analyzing the nature of gear selection in the Hawaiian deep-sea handline fishery demonstrates two basic points. In all six situations examined, the day fished had a highly significant effect on the variables measured, whereas in only one case out of eight was a significant effect due to hook size demonstrated (Table 1). It is important to realize that the range of hook sizes used here is fairly typical of those in the fishery although hooks smaller than this series are occasionally employed.

Based on these facts it is reasonable to conclude that alterations in gear within this range of sizes have very little effect on the outcome of bottom fishing in Hawaii. It is readily apparent that variation in both catch rates and species size composition within this fishery are caused predominantly by differences between fishing banks, months, and days (replications). This variation is more than enough to mask any real hook effects at the present level of sampling, although in one situation (number of opakapaka) a significant effect due to hooks was revealed.

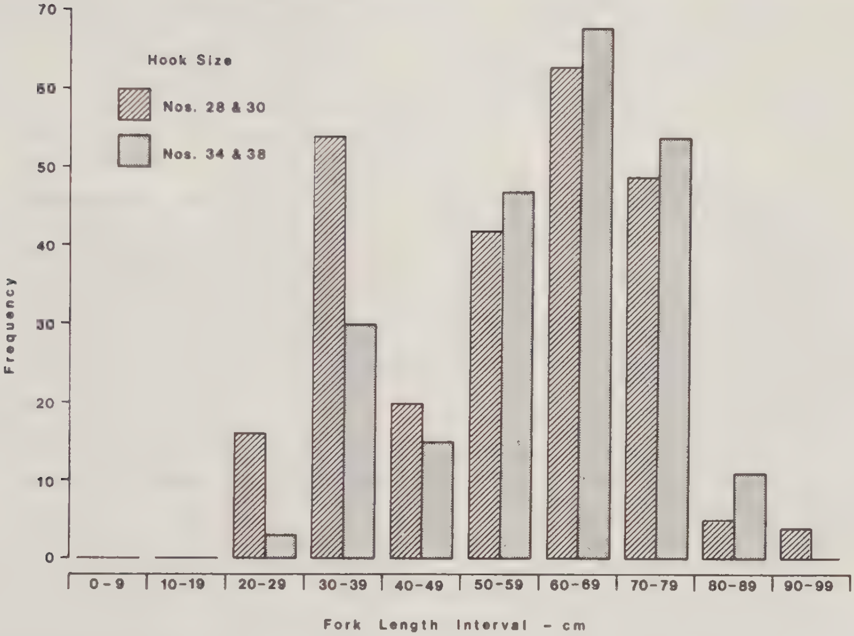

FIG. 2. Combined length–frequency distributions of opakapaka, hapuupuu, and pig ulua which are pooled according to capture on small hooks (Nos. 28 and 30) or large hooks (Nos. 34 and 38).

That the hook-and-line fishery is relatively insensitive to moderate changes in gear is contrary to expectation if the selection curve for hooks were dome shaped. Thus, it is reasonable to presume that in this fishery, selection by hooks is better described by a trawl type or sigmoidal selection curve, with little differential sampling of the larger individuals in the population (e.g. Chatwin 1958; McCracken 1963; Saetersdal 1963). This presumption is supported by the data presented in Fig. 2. Here the combined catches of opakapaka, hapuupuu, and pig ulua have been pooled into two groups: those fish caught on large hooks (Nos. 34 and 38) and those caught on small hooks (Nos. 28 and 30). The histograms suggest that for medium- and large-sized fish (≥45 cm FL) the large and small hooks draw more or less equivalent samples. However, the small hooks appear to have been more effective in capturing small fish (<45 cm FL). These results are compatible with the hypothesis that the selection curve for hooks is sigmoidal. For these reasons it is reasonable to conclude that the catch of bottom fish ≥45 cm FL is likely to be representative of the population sampled.

If a sigmoidal selection curve is postulated for this hook-and-line gear, there should exist a minimum size of capture. That the mean size landed for each species, when treated individually, was insensitive to changes in hook size (Table 1) is contrary to the findings of both McCracken (1963) and Saetersdal (1963). This discrepancy could be due to constraints imposed on the sampling process by the behavior of the fish (see for example Allen 1963). A more likely explanation is insufficient sampling.

Furthermore, the range of hook sizes which were utilized in these experiments (Fig. 1) was not broad. If hooks spanning a greater size range had been employed, it is more likely that a treatment effect on mean size of capture would have been conclusively demonstrated for each species. For example, it is possible to compute an index which measures the size range of hooks used by forming the ratio of the absolute sizes of the largest hook used to the smallest. Hook size is calculated as the product of the length and width of a hook (Fig. 1). In this study the largest hook used (No. 38) was 71% greater in size than the smallest hook (No. 28). In contrast, Koike et al. (1968) and Kanda et al. (1978) used series of hooks in which the largest sizes were 215 and 111%, respectively, larger than the smallest of sizes. Both studies reported shifts in the size composition of the catch depending upon the size of hooks used. Clearly, if hook sizes are highly dissimilar the size composition of the catch must ultimately vary. In spite of this, the hook sizes I used are typically those in use by the fishermen. Moreover, Saetersdal (1963) reported a change in the selective characteristics of fishing hooks which differed in size by only 76%. Consequently, it may be concluded that within the context of the Hawaiian deep-sea handline fishery, little size bias attributable to hook-and-line gear manifests itself in the catch of bottom fish.

Acknowledgments

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A MULTISPECIES ANALYSIS OF THE COMMERCIAL DEEP-SEA HANDLINE FISHERY IN HAWAII

STEPHEN RALSTON[1] AND JEFFREY J. POLOVINA[2]

ABSTRACT

In the Hawaiian Islands 13 species of bottom fish are commonly harvested in the commercial deep-sea handline fishery. These are all high-level carnivores, including snappers, jacks, and a species of grouper, which are sought in water depths ranging from 60 to 350 m. Cluster analyses performed on the Hawaii Division of Fish and Game commercial catch report data suggest the existence of three bottom fish species groups which apparently segregate on the basis of depth distribution. These groups seem to be stable through time and similar among differing geographic localities.

Two measures of fishing effort, catch-records and fisherman-days, were compared to determine which is more suitable for use in stock-production analyses. Fisherman-days was selected because, among other reasons, it repeatedly demonstrates a stronger negative correlation with catch per unit effort.

Application of the Schaefer stock-production model to this multispecies fishery on a species-by-species basis provides an inadequate description of productivity. When catch statistics are aggregated according to the three cluster analysis species groups the results are much improved. In this regard consistently significant results and production estimates were obtained from the Maui-Lanai-Kahoolawe-Molokai bank, a region which presently accounts for about half of the total Hawaii catch. No significant interaction among the cluster groups was detected. When all 13 bottom fish species are analyzed together, the results are in agreement with the preceding analysis. Examining the aggregation process suggests that the model based on the intermediate level of aggregation (cluster groups) explains slightly more of the variation in total catch than does the model which treats all 13 species together.

We estimate the annual maximum sustainable yield of the commercial deep-sea handline fishery around the Maui-Lanai-Kahoolawe-Molokai bank to be 106 metric tons or about 272 kg/nmi of 100-fathom isobath. Because recreational catch is unaccounted for these figures are considered lower bounds for the gross production obtainable from this type of fishery although currently the commercial fishery is operating close to this maximum-sustainable-yield level.

Effective management programs for tropical fisheries are difficult to achieve (Pauly 1979). Often attempts at managing these fisheries are based on the application of inappropriate models to sparse data. Both deficiencies are due in part to the multiplicity of fish species inhabiting tropical environments. This great diversity (Sale 1977; Talbot et al. 1979) makes it difficult to compile adequate data for all species of interest. The Hawaiian Islands, which straddle the Tropic of Cancer, possess a relatively impoverished tropical ichthyofauna, yet between 600 and 700 species are known from this region (Gosline and Brock 1960). Coupled with high diversity, many tropical countries lack a refined statistical system for the acquisition and storage of fisheries data. In concert these two limitations impose severe restrictions on the quantity and quality of data which are currently available for the analysis and management of tropical fisheries (Pope 1979). Furthermore, classical fisheries models thus far developed have been directed toward the management of temperate and boreal stocks (Food and Agriculture Organization of the United Nations (FAO) 1978). These models usually treat species as independent management units. It has become apparent that such an approach is often inadequate when extrapolated to the tropics where community dynamics become increasingly important (Pauly 1979).

The multispecies approach to managing fisheries exploitation in complex ecosystems has only recently acquired a substantive base in the literature. Early work by Larkin (1963, 1966)

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[1] Fisheries Research Institute, College of Fisheries, University of Washington, Seattle, Wash.; present address: Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[2] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

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evaluated the consequences of Lotka-Volterra competition and predator-prey systems on optimum exploitation strategies. Paulik et al. (1967) examined the problem of maximizing the yield from a fishery composed of mixed stocks, each with a unique spawner-recruit curve. A large body of descriptive work has documented the successional nature of changing catch composition which is often characteristic of increasing exploitation in a multispecies fishery (e.g., Regier 1973). Several recent multispecies investigations present highly sophisticated ecosystem models that require numerical solution and/or dynamic simulation, as well as numerous parameter estimates (Parrish 1975; Andersen and Ursin 1977; Laevastu and Favorite 1978[3]).

An alternative to this latter approach simply treats multispecies fisheries as though they behave as would a single species stock and evaluates production by application of the total biomass Schaefer model (TBSM) (Pope 1979). Brown et al. (1976) estimated total finfish production in the northwest Atlantic in this manner, as did Brander (1977) for demersal fish and shellfish in the Irish Sea. A review of this approach shows that "these overall Schaefer models generally seem to fit the data rather better than the fits experienced with their component stocks" (FAO 1978). Among the possible reasons for this are 1) the TBSM really presents a more realistic representation of multispecies fisheries than does summing the yields of individual stocks, 2) the better fit results from some type of averaging process, 3) artifacts in the method of fitting and/or shifts in preference between species within a fishery may result in a better fit when total biomass is evaluated (FAO 1978; Pauly 1979; Pope 1979). Several authors have issued the caveat that a thorough understanding of trophic relations is fundamental to managing any multispecies fishery and that such considerations may easily invalidate the application of the TBSM (May et al. 1979; Pauly 1979).

This paper estimates the productivity of deep-dwelling bottom fish stocks around the main islands of the Hawaiian Archipelago using stock-production methods. The fishery for these stocks is conducted in offshore waters ranging in depth from 60 to 350 m where a variety of species, principally snappers of the Family Lutjanidae, abound. In addition to providing preliminary productivity estimates for this fishery, an examination of the performance of the TBSM at various levels of species aggregation is undertaken. This latter analysis provides a quasi-quantitative means of evaluating the applicability of the TBSM to the Hawaiian offshore handline fishery.

SOURCES OF DATA AND DESCRIPTION OF THE FISHERY

In the State of Hawaii, all fishermen who sell a portion of their catch must be licensed as commercial fishermen by the Hawaii Division of Fish and Game (HDFG). There is no licensing requirement for recreational fishing. New commercial licenses are issued every fiscal year and once licensed, fishermen are required to submit a monthly catch report whether or not they have fished. These monthly catch reports require from each fisherman entries on the days and areas in which he fished, the types of fishing gear used, the number of individuals and pounds of the different species landed, and the dollar value of the catch. Incomplete reporting is thought to be common and raises the question of bias in the data (Ralston 1979[4]). Perhaps more serious is the omission of any direct measure of fishing effort or fishing power in the information concerning bottom fish obtained from these reports.

Monthly catch reports are coded, keypunched, and stored on magnetic tape for future use by HDFG. These data are the basis of this study and currently span the 20-yr period 1959 to 1978 inclusive, comprising some 600,000 records. While the date are voluminous, the extent of nonreporting by recreational fishermen and of incomplete or underreporting by commercial fishermen is unknown.

The complete HDFG data account for all types of commercial fishing in the State of Hawaii; therefore, only those catch records which list deep-sea handline fishing gear were used in this study. This reduced the data to one-fourth its original size and defined the scope of the fishery. Although the name suggests otherwise, the fishing gear is primarily hydraulic or electric although some manual equipment remains in use.

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[3] Laevastu, T., and F. Favorite. 1978. Numerical evaluation of marine ecosystems. Part 1. Deterministic bulk biomass model (BBM). NWAFC Process. Rep., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash., 22 p. (Unpubl. rep.)

[4] Ralston, S. 1979. A description of the bottomfish fisheries of Hawaii, American Samoa, Guam, and the Northern Marianas. A report submitted to the Western Pacific Regional Fishery Management Council, Honolulu, 102 p. (Unpubl. rep.)

The fishery mainly exploits 13 categories of fish species (Table 1). Confusion concerning the taxonomy of species in the family Carangidae prohibits a more detailed classification of these forms although *Pseudocaranx dentex* and *Caranx ignobilis* probably account for the majority of ulua landed in Hawaii. While *P. dentex* is abundant in the Northwestern Hawaiian Islands, it is apparently uncommon around the main high islands (Uchida[5]). Further confusion is apt to result from the findings of Anderson (1981), who recently revised the genus *Etelis* and changed the names of both Hawaiian species. In addition, two hogfish species are frequently taken, *Bodianus bilunulatus* and *B. vulpinus*, although the former species seems to inhabit somewhat shallower depths than the latter. Of those species listed, most are caught almost exclusively with deep-sea handline gear. The exceptions are ta'ape, ulua, and a'awa which are commonly taken by several other methods (e.g., inshore handline, purse seine, gill net, etc.) (Ralston footnote 4). Catches of these species reported here include only those portions taken in the offshore handline fishery.

TABLE 1.—Principal species of fish landed in the Hawaiian offshore handline fishery.

Family	Species	Common name	Average weight (kg)
Lutjanidae	*Aphareus rutilans*	Lehi	3-8
	Aprion virescens	Uku	2-8
	Etelis coruscans	Onaga	2-8
	E. carbunculus	Ehu	0.5-2
	Lutjanus kasmira	Ta'ape	0.5
	Pristipomoides filamentosus	Opakapaka	1-6
	P. sieboldii	Kalekale	0.5
	P. zonatus	Gindai	0.5-2
Carangidae	*Caranx* and *Carangoides* spp.	Ulua	1-10
	Seriola dumerili	Kahala	3-10
Serranidae	*Epinephelus quernus*	Hapu'upu'u	3-10
Labridae	*Bodianus* spp.	A'awa	1-3
Scorpaenidae	*Pontinus macrocephala*	Nohu	1-2

In descending order the dominant species in the fishery by weight are the opakapaka, ulua, uku, onaga, hapu'upu'u, and kahala (Ralston footnote 4). These species taken together accounted for 86% of the total catch by weight in 1978, nearly all of which was marketed in Hawaii as fresh fish. Total landings from the fishery have remained relatively constant from 1959 to 1978, showing a slight increase in recent years, although higher catches were briefly reported during the late 1940's and early 1950's (Fig. 1) (Ralston footnote 4). Most of these species are highly prized and in recent years have averaged close to $5.00/kg ex-vessel.

In the past about 85% of the catch of deep dwelling bottom fish has been made around the main Hawaiian Islands in contrast to the uninhabited Northwestern Hawaiian Islands (Grigg and Pfund 1980). Catches from the latter area have increased remarkably in the last 2 yr, as larger, more seaworthy vessels have entered the fishery. Nonetheless, the lack of sufficient data

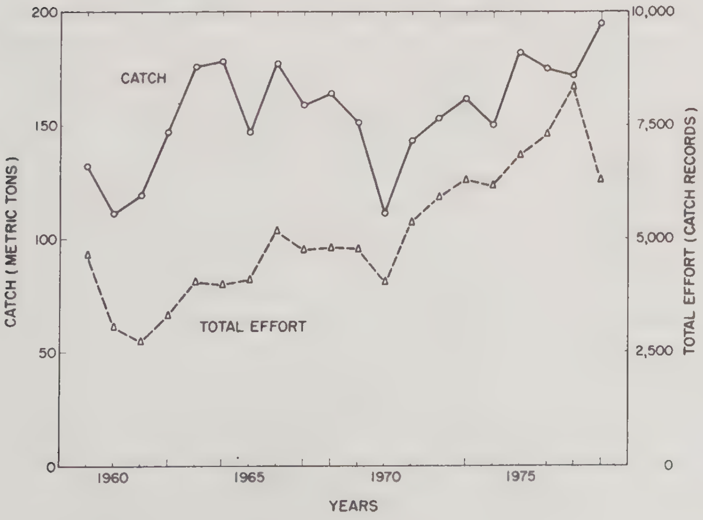

FIGURE 1.—Annual landings and total annual effort for the commercial deep-sea handline fishery in the main high islands of the Hawaiian Archipelago.

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[5] R. N. Uchida, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. commun. November 1980.

from this region prevents its analysis; the results presented here pertain only to the eight main islands of the archipelago (Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, and Niihau, including Kaula Rock). Within this region fishing is conducted on offshore banks and pinnacles, primarily in the vicinity of the 100-fathom isobath. In the Hawaiian Islands the sea bottom typically extends away from shore at a depth of 30 fathoms for some distance and then falls abruptly to very great depths over a relatively short horizontal span (Brock and Chamberlain 1968). Most fishing occurs in this steep dropoff zone. Hence it is possible to crudely estimate the relative amount of total bottom fish habitat around a fishing bank by determining the length of the 100-fathom isobath surrounding it (Table 2). The maximum depth between the islands of Maui, Lanai, Kahoolawe, and Molokai (MLKM) is <100 fathoms; therefore, they were pooled and treated as a single bank (Fig. 2). All bottom fish taken from a bank were considered one stock because movements of juveniles and adults across deep water from one bank to the next are highly improbable whereas lateral movements around the perimeter of the 100-fathom isobath of a bank cannot be discounted. The Islands of Oahu and Hawaii are separated by deep water from all other islands and banks, hence, by definition, they harbor distinct stocks. Kauai, Niihau, and Kaula Rock (KNK), although separated across short distances by deep water, were analyzed together because they present a similar fishing profile and they are closely situated to one another. Thus, based on this classification four distinct stocks were analyzed independently. The extent of larval dispersal between these stocks is unknown at present but is currently under study (Shaklee[6]). A more detailed description of this fishery may be found in Ralston (footnote 4) or in Hawaii Department of Land and Natural Resources (1979).

TABLE 2.—A list of the four banks which harbor separately defined stocks. The length of the 100-fathom isobath around a bank roughly measures the extent of its bottom fish habitat.

Bank	Percent contribution to total landings	Approximate length of 100-fathom isobath (nmi)
Hawaii	21	290
MLKM[1]	56	390
Oahu	12	150
KNK[2]	11	195

[1] Maui-Lanai-Kahoolawe-Molokai.
[2] Kauai, Niihau, and Kaula Rock.

FISHING EFFORT

The ultimate goal of any stock-production analysis is to relate the impact of variable fishing pressure on stock abundance. Fishing pressure

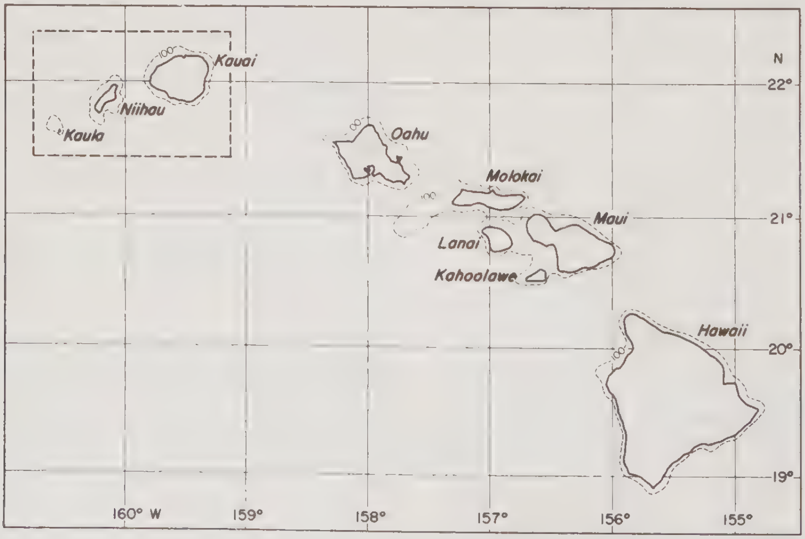

FIGURE 2.—Map of the eight main Hawaiian Islands and Kaula Rock with the 100-fathom isobath included.

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[6] J. G. Shaklee, Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI 96744, pers. commun. 1979.

is most conveniently formulated as instantaneous fishing mortality (F), measured over some arbitrary interval of time, usually 1 yr (Ricker 1975). Frequently it is not possible to measure F directly, however, and so a proportionate measure of F is selected, i.e., fishing effort or f. The ideal choice of units for fishing effort results in a linear correspondence between F and f, a zero intercept, and minimal residual variance (Rothschild 1977). Because F is frequently unknown, it is often difficult to ascertain whether these criteria are met and yet the selection of an appropriate measure of fishing effort is most critical to meeting the assumptions of a stock-production analysis. Ample consideration should be given to these factors before the data are collected.

No attempt has been made in the HDFG data to record either the fishing effort or the fishing power of individual fishermen. A suitable measure of fishing mortality in this fishery would be the cumulative number of hook-hours or line-hours of fishing. While such figures are currently unavailable, it has been possible to determine the total number of fishing records filed in a year which report the catch of a particular species. This statistic, the number of daily reports by fishermen who have caught any one particular species, was frequently computed and is termed catch-records. Figure 1 presents, in addition to the catch, the total number of deep-sea handline catch-records filed from 1959 to 1978 concerning all 13 species of bottom fish. This measure of fishing effort does not always correspond to the number of fisherman-days because one operator may catch several species during a single day of fishing. In this instance the reporting of each particular species comprises one catch-record. Thus, when aggregated species groups are considered, the number of fisherman-days will always be fewer than the total number of catch-records. When species are considered independently of one another the two figures are equal (catch-records = fisherman-days).

Interpreting the meaning of a fisherman-day as a unit of fishing effort in this fishery is difficult. It was tabulated by following the daily reports of individual fishermen, identified by their commercial fishing license numbers. All commercial fishermen in Hawaii, whether captain or crew, must have a license. It is likely that many catch reports are filed only by boat captains who document the landings of an entire fishing vessel, which may have a variable number of crew members. Thus a fisherman-day, as defined here, may reasonably be thought of as a vessel-day. However, because this unit of effort is defined and specified on the basis of commercial fishing licenses, in the interests of exactitude, we have chosen to use the term fisherman-day.

RESULTS

Clustering

The usual method of aggregating catch data would be to pool all 13 deep-sea handline species into a single group and to analyze the total with the TBSM. An alternative is to employ a multivariate statistical procedure to assess the degree of colinearity among species and to define species groups based on the strength of interspecies associations in the catch (Pope 1979). Such an approach would identify those bottom fish which tended to appear with one another in the catch to the exclusion of others and would measure the extent of correlation of fishing mortality among species. Pope (1979) has termed this "technological interaction" and has discussed its importance in multispecies fisheries. Separate application of the TBSM to each species group formed by clustering would constitute an analysis performed at an intermediate level of species aggregation. Conceptually this is desirable because in the Hawaiian offshore handline fishery different species are known to exhibit stratification by depth (Strasburg et al. 1968).

Cluster analyses were performed with a computer routine (Dixon 1977, program P1M) where the 13 species of bottom fish comprised the variables to be clustered and the catch from a single day's fishing formed one case. Associations were computed on the basis of the landed weight of each species. The average linkage between groups defined the criterion for amalgamating clusters and correlation coefficients were used as measures of similarity.

Separate analyses were performed for each of the four designated bank (Table 2) areas to assess whether obvious differences exist among banks with regard to interspecies associations. Similarly, separate analyses were conducted for the years 1959, 1965, 1971, and 1977 to see whether temporal variation in species grouping is an important factor to consider.

No striking differences or patterns emerged from these various comparisons. The intrinsic variation apparent between clusters obtained from the same bank in 3 adjacent years (Hawaii in 1976, 1977, and 1978) was as great as the variation in clustering found between different banks and through longer periods of time. While there were a few suggestions of differences in the species composition of groups among the four banks, these were relatively minor and were ignored. Only one fairly consistent pattern of grouping was repeatedly exhibited across banks and through time, and this was confirmed by a single clustering of all the data pooled together. This pattern shows that the bottom fish fishery is loosely composed of three species groups which are apparently segregated on the basis of the depth range of member species (Table 3) (for depth distributions see Gosline and Brock 1960; Brock and Chamberlain 1968; Strasburg et al. 1968). These groups represent species assemblages which are for the most part independent of time and/or geographic location.

The delimitation of these three species groups is somewhat arbitrary and should not be viewed as the only way in which an intermediate level of species aggregation of the catch could be achieved. Nevertheless this grouping structure is reasonable and its use enhances the biological realism of the multispecies model by identifying and classifying those species which seem to share the greatest correlation in fishing mortalities. In addition the grouping structure allows an assessment of the effect aggregation has on the fit of data to a Schaefer stock-production analysis. A brief discussion of each of these groups is appropriate.

The appearance of ulua, ta'ape, and a'awa in the shallowest group (Group I) is consistent with the observation that these three species are frequently harvested with other types of fishing gear. Members of this group are often seen by scuba divers who venture below 30 m, although the vertical distribution of these species in the deep-sea handline fishery is centered around the 60 m terrace which circles much of the Hawaiian Islands (Brock and Chamberlain 1968). Because the name ulua refers to several different carangid species, one of which (*P. dentex*) is most often taken with members of Group II in deeper water, it is evident that some inaccuracies in the classification exist. This particular defect is not so much a result of the clustering process as it is a result of faulty data. Kahala, on the other hand, range widely (Gosline and Brock 1960) and are known from throughout the depth ranges of both Groups I and II and occur even shallower. Its position in Group II may simply reflect the relatively greater fishing pressure exerted in the 100-200 m depth range where other members of Group II, such as the opakapaka and hapu'upu'u, are centered. The deepest group (Group III) is particularly well defined and is composed of three lutjanid species, two of which are deepwater eteline red snappers.

TABLE 3.—Bottom fish species groupings defined by cluster analysis.

Group	Species	Approximate depth range (m)
I	Ulua, uku, ta'ape, a'awa	30-140
II	Opakapaka, hapu'upu'u, kahala, gindai, lehi, nohu	80-240
III	Onaga, ehu, kalekale	200-350

Fishing Effort

An attempt was made to evaluate the two measures of fishing effort, catch-records and fisherman-days, on the basis of their correlation with catch per unit of effort (CPUE). The Schaefer model predicts that plots of CPUE against effort should demonstrate a linear relationship with a negative slope if the production of the stock is described by the logistic growth curve (Ricker 1975). Such a prediction generates a one-tailed test of the hypothesis that $\rho \geq 0$ against the alternative hypothesis that $\rho < 0$ where ρ is the population correlation coefficient between CPUE and f. Even though a negative correlation between CPUE and effort is expected in a situation where catch and effort are completely unrelated random variables, the degree of spurious correlation due to this effect will be small if the main cause of variation in CPUE is varying stock abundance (Gulland 1974).

Correlations were computed between these two variables, using both measures of fishing effort for each species group-bank combination ($3 \times 4 = 12$). Additional correlations were computed for the total aggregated catch from each of the four banks ($1 \times 4 = 4$), resulting in 16 comparisons of the two measures of effort (Table 4). Comparisons which might be based on treating species as independent stocks are inappropriate here because the two measures of effort become equal in this limiting case. One means of evaluating the effectiveness of these two measures is to compare the signs of the correlation coefficients (r) and the magnitudes of the coefficients of determination (r^2) for each. It

TABLE 4.—Comparisons of correlations of CPUE and fishing effort (f) for two different measures of f. The total aggregate incorporates all 13 species.

		Unit of fishing effort			
		Catch-records		Fisherman-days	
Group	Bank[1]	r	r^2	r	r^2
I	Hawaii	−0.095	0.01	−0.128	0.02
	MLKM	−0.358	0.13	[2]−0.503	0.25
	Oahu	−0.153	0.02	−0.259	0.07
	KNK	−0.180	0.03	−0.111	0.01
II	Hawaii	−0.111	0.01	−0.120	0.01
	MLKM	−0.379	0.14	[2]−0.769	0.59
	Oahu	+0.285	0.08	+0.293	0.09
	KNK	+0.481	0.23	+0.237	0.06
III	Hawaii	−0.187	0.03	−0.015	0.00
	MLKM	−0.240	0.06	[2]−0.502	0.25
	Oahu	−0.362	0.13	[2]−0.390	0.15
	KNK	−0.308	0.09	[2]−0.395	0.16
Total aggregate					
	Hawaii	−0.150	0.02	−0.334	0.11
	MLKM	[2]−0.463	0.21	[2]−0.878	0.77
	Oahu	[2]−0.465	0.22	[2]−0.521	0.27
	KNK	+0.395	0.16	−0.165	0.03

[1] MLKM = Maui-Lanai-Kahoolawe-Molokai
KNK= Kauai, Niihau, and Kaula Rock.

[2] Significant at $P = 0.05$ level, one-tailed test, df = 18.

is apparent that in 13 of the 16 possible comparisons, fisherman-days showed a stronger negative correlation with CPUE than did catch-records. Based on these results we conclude that fisherman-days predicts the behavior of CPUE more precisely than catch-records. Use of this measure also eliminates repeated counting of effort statistics when more than one species in a group is caught on a particular day and has greater intuitive appeal as well. For these reasons we conclude that fisherman-days is the best measure of fishing effort available at present. It is worth noting that these two different measures of effort are approximately linear in their relationship to one another, implying that the superiority of fisherman-days over catch-records as a measure of effort is probably due to a smaller residual variance of instantaneous fishing mortality (F) on the former statistic than on the latter.

Stock Production Analyses

In this section the Schaefer model is applied to the deep-sea handline data in which the catch is aggregated at three different levels. At the first level a single-species Schaefer model is fitted to each species separately. Next, the TBSM is fitted to each of the three species groups delimited by the cluster analysis. In the final section the total aggregated catch of all 13 species taken together is analyzed with the TBSM. Fisherman-days was used as the measure of fishing effort throughout, but equilibrium approximation (Gulland 1972) was not attempted because no information was available concerning the longevity of these species and a previous application of this method to the data had shown little improvement in the results (Ralston footnote 4).

When each species is treated independently there are 52 separate analyses (4 banks with 13 species each). In only two of these regressions of CPUE on f is the null hypothesis $\beta \geq 0$, where β is the slope of the regression, rejected in favor of the alternative hypothesis $\beta < 0$. Both involved the MLKM bank where opakapaka ($t = -2.91$, df = 18) and uku ($t = -1.82$, df = 18) demonstrated significant inverse regressions in which respectively, 32% and 16% of the total variation in CPUE were explained. The significance of these two regressions can easily be attributed to the Type I error and consequently nothing can be concluded from these results concerning the productivity of these fishes.

The fit of the TBSM to the data is much improved when the three species groups are considered. The model was applied to the HDFG data 12 times; once for each species group and bank combination. Significant results ($P = 0.05$, one-tailed test) were obtained in 5 of the 12 applications of the model (Table 5). The three analyses from the MLKM bank were significant in every case and those for Group III were significant in three out of the four regressions tested. The observation that the results from the remaining banks and species groups are not significant is not so disturbing because 56% of all bottom fish landings are harvested from the MLKM bank (Table 2). An estimate of the maximum sustainable yield (MSY) and optimum effort was then computed for each of the five significant combinations, as well as a standardized measure of productivity, calculated as the sustainable yield of bottom fish per nautical mile of 100-fathom isobath. Assuming logistic growth of the stocks the catchability coefficient was estimated using the computer program PRODFIT (Fox 1975). The t value in the table refers to the test of the null hypothesis that the slope of a regression is zero or positive.

Pope (1979) has proposed an interactive model to describe multispecies fisheries in which total yield is depicted as the sum of the yields of individual species with additional terms to account for community interactions. In the simple two-species case the equation describing surplus production (Y) is:

TABLE 5.—Significant applications of the total biomass Schaefer model to the Hawaii Division of Fish and Game data set where species have been aggregated according to cluster analysis species groupings.

Bank[1]	Species group	MSY[2] (kg/yr)	Optimum effort (fisherman-days)	MSY/nmi 100-fathom isobath	Catchability coefficient	t value (df = 18)
MLKM	I	23,000	480	60	0.00180	−2.47
	II	48,800	662	125	0.00062	−5.11
	III	31,900	396	82	0.00120	−2.46
Oahu	III	1,900	119	12	0.00280	−1.74
KNK	III	4,800	84	25	0.00600	−1.77

[1] MLKM = Maui-Lanai-Kahoolawe-Molokai
KNK = Kauai, Niihau, and Kaula Rock.
[2] MSY = maximum sustainable yield.

$$Y = a_1N_1 + a_2N_2 - b_1N_1^2 - b_2N_2^2 + (c_1 + c_2)N_1N_2 \qquad (1)$$

where N_1 and N_2 refer to the population sizes of species one and two and a_1, a_2, b_1, b_2, c_1, and c_2 are model parameters (Pope 1979). This model is the sum of two single-species surplus production models with the additional term $(c_1 + c_2)N_1N_2$ to account for the interaction between the two species. Depending upon the signs of c_1 and c_2 the equation models predation, competition, or mutualism. More importantly, the sum of these two parameters determines the impact of the interaction on the sustainable yield of the system.

The question of whether significant interaction occurs among the cluster-analysis species groups was examined by considering the MLKM bank alone. The regressions of all three cluster groups were highly significant from this region and further treatment of these data is therefore considered appropriate.

In the three-species version of Equation (1) there are three terms involving the sum of c parameters. In this analysis a species group (I, II, or III) is treated as though it were a single species and the a and b parameters necessary to evaluate the equation were taken from the independently calculated regressions of Table 5. A nonlinear regression routine (SAS Institute 1979, program NLIN) was employed to estimate the sums of the various c parameters for the MLKM bank (Table 6). It is apparent that these sums do not differ significantly from zero and hence there is no evidence for significant interaction among groups. This result further supports the classification of species into independent assemblages for use in an aggregated treatment of the data.

TABLE 6.—Tests of whether interaction between cluster analysis species groups have a significant effect on total bottom fish yield from the Maui-Lanai-Kahoolawe-Molokai bank.

Term	Parameters	Evaluated value	95% confidence limits
$(c_1 + c_2)\ N_1N_2$	$(c_1 + c_2)$	0.242	(−0.244, 0.728)
$(c_2 + c_3)\ N_2N_3$	$(c_2 + c_3)$	0.185	(−0.284, 0.654)
$(c_1 + c_3)\ N_1N_3$	$(c_1 + c_3)$	−0.868	(−2.365, 0.629)

In the final analysis all species were treated as a single group and the TBSM was applied to the total aggregate. Of the four possible regressions of CPUE on f, both the MLKM and Oahu banks yielded significant results (Table 7). Similar computations were performed for these sites as had been done previously. In addition the regression of total bottom fish CPUE on f for the MLKM bank and the corresponding catch curve (catch versus effort) were plotted (Fig. 3). It is reassuring to note that the sum of the three-species group MSY's from this bank, calculated from the preceding analysis, amounts to 103,700 kg/yr. This estimate compares favorably with the present result (a difference of about 2%) though the two figures were computed somewhat independently. A comparison of MSY/nmi 100-fathom isobath between these two banks reveals the Oahu value to be substantially less than the MLKM value. Although this may in actuality represent differences in habitat quality and productivity between these banks, there is the possibility that the difference is at least partially due to a difference in the extent of unreported recreational fishing pressure between the banks.

The results of the stock-production analysis for the MLKM bank provide statistically acceptable regressions, yet the estimates of production are

TABLE 7.—Significant applications of the total biomass Schaefer model to the Hawaii Division of Fish and Game data set where all species have been grouped into one total aggregate.

	Bank	
	MLKM[1]	Oahu
MSY[2] (kg/yr)	106,000	15,700
Optimum effort (fisherman-days)	901	424
MSY/nmi, 100-fathom isobath	272	105
Catchability coefficient	0.00080	0.00168
t value (df = 18)	−7.77	−2.59

[1] MLKM = Maui-Lanai-Kahoolawe-Molokai.
[2] MSY = maximum sustainable yield.

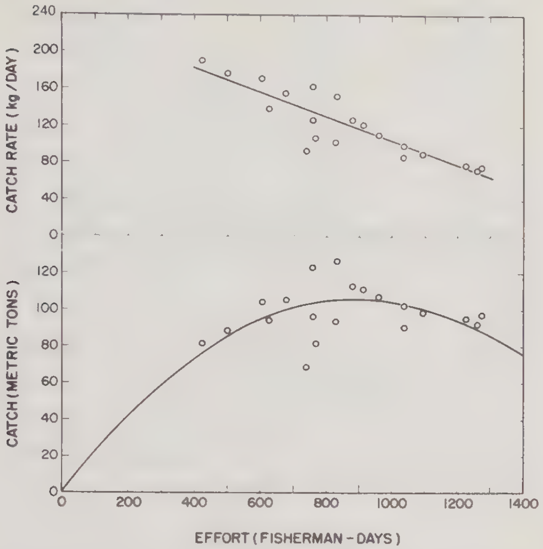

FIGURE 3.—Fitted production curves of CPUE and catch on fishing effort for the total aggregate landings of commercial bottom fish species from the Maui-Lanai-Kahoolawe-Molokai bank.

probably low. The HDFG data provide information on only a portion of the harvest of these species. Recreational bottom fishing is very popular around the main islands of the Hawaiian Archipelago but its relative impact is completely unknown. Furthermore, underreporting by commercial fishermen is also likely but its extent is hard to determine. Based on these considerations, the overall estimate of annual production calculated for the MLKM bank (272 kg bottom fish/nmi 100-fathom isobath) is best considered a lower bound for the surplus production obtainable from this type of fishery. In spite of the difficulty in determining precise estimates of productivity it would appear that the added effects of commercial and recreational fishing are close to fully exploiting the fishery (Fig. 3). In 1978 over 96 t (metric tons) of bottom fish were harvested from the MLKM bank by commercial fishermen.

DISCUSSION

Fishing Effort

One of the primary goals of this study has been to estimate the commercial productivity of Hawaii's offshore bottom fish resources. We have met with mixed success in our attempt because only one of the four study banks (Fig. 2) consistently provided significant results. In spite of this difficulty the MLKM is the largest of the four, producing well over half the total catch of bottom fish. The lack of statistical significance from the remaining banks may be due to several factors.

The impact of fishing is measured by correlating changes in fishing effort with catch rate (CPUE). If the observed range of fishing effort is too small to render an appreciable change in stock density then the impact of fishing cannot be measured. This hypothesis of insufficient variation in fishing mortality does not explain the lack of correlation between CPUE and effort from the Hawaii, Oahu, and KNK banks, however. The range in fishing intensity (defined as fisherman-days/nmi 100-fathom isobath or fishing effort per unit area) between the period 1959 and 1978 was the least for the MLKM bank where only a threefold difference in intensity was experienced. In contrast, fishing intensities ranged upwards from 4-fold (KNK) to 26-fold (Oahu) among the remaining banks. The range of fishing intensity to which the MLKM bank has been exposed is the least of all four sites and from this observation it would be reasonable to assume that all banks have experienced substantial variation in fishing mortality.

This follows logically only if the catchability coefficients for all banks are similar. It is probable, however, that these four regions differ with respect to the impact of one unit of fishing effort on the various stocks. If differences in fishable area are corrected for, a fisherman-day recorded from Oahu may well represent less fishing mortality than the same figure from the MLKM bank. In this regard, preliminary analyses based on fishing intensity rather than fishing effort showed that significant differences exist among the four banks in the relationship of CPUE to fishing intensity, precluding the option of pooling the data across banks (see Munro 1978 for a production analysis based on fishing intensity). In principle then, differences in catchability could explain the poor results from Hawaii, Oahu, and KNK if the catchability coefficient equating fisherman-days to fishing mortality from these areas is substantially less than that for MLKM. Variation in the extent of unreported catch among banks could compound this effect.

Other factors which remain unaccounted for could further confound the interpretation of effort statistics. It is unknown whether the percentage of reported catch to total catch, among both commercial and recreational fishermen, is increasing, decreasing, or remaining stable. There has also been a trend toward increased fishing power with the advent of mechanical line haulers, but the exact amount of this effect is unknown. Considerations such as these make it difficult to quantify bottom fish effort statistics.

This brief discussion underscores the importance of employing an appropriate measure of fishing effort in which catchability does not vary according to the activities of man. It was possible to demonstrate the superiority of fisherman-days over catch records and yet the former measure proved to be inadequate when pooling across banks was attempted.

Effects of Aggregation

Investigators have reported that in a multispecies fishery the TBSM when applied to aggregated data often fits better than the Schaefer model applied on a species-by-species basis (FAO 1978; Pauly 1979; Pope 1979). We will examine this phenomenon for data from the MLKM bank for two levels of aggregation.

As shown in the results section we have applied the Schaefer model to CPUE and effort data at three levels of data aggregation. First we applied the Schaefer model to the data on a species-by-species basis. Then species were partitioned into three cluster groups, the catch and effort data were computed for each group, and the TBSM was fitted to each group. Finally all species were pooled into one group and the aggregate data consisting of total catch and effort were computed and fitted with the TBSM.

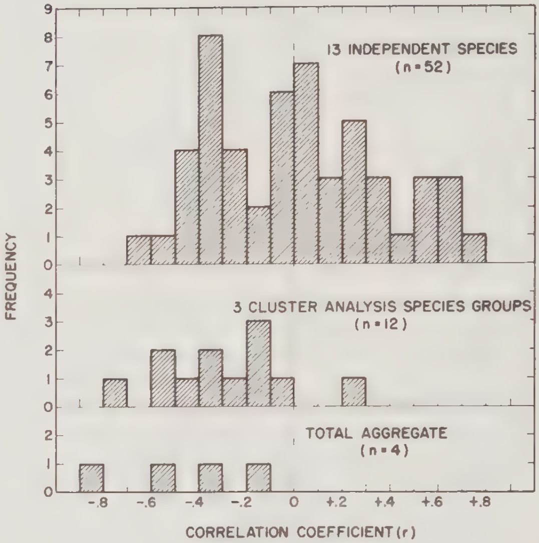

FIGURE 4.—Frequency distributions of correlation of coefficients between CPUE and fishing effort based on three levels of species aggregation.

The fit of the TBSM to each of the three species groups and to the total group resulted in significant regressions for the MLKM bank while only 2 out of 13 single-species regressions for this bank were significant. This result may be due to the fact that the fishery exploits groups of species simultaneously and that our measure of fishing effort measures exploitation on species groups rather than single species. It is apparent that when the data in this study were progressively pooled, the correlation coefficients describing the fit became increasingly negative (Fig. 4). This result alone would suggest that aggregation led to a better fit. Unfortunately because only 2 out of the 13 single-species regressions were signficant, it is not appropriate to use the single-species results in our comparison of the effects of aggregation. Table 4 presents the correlation coefficients between CPUE and effort for each of the three cluster groups and the total aggregate. At first glance it appears that for the MLKM bank the TBSM applied to the total group fits substantially better ($r^2 = 0.77$ for fisherman-days) than the TBSM applied to any of the three species groups ($r^2 = 0.25$, $r^2 = 0.59$, and $r^2 = 0.25$). However, an examination of the correlations between fishing effort for the three cluster groups reveals that these variables are highly correlated (Table 8). Grunfeld and Griliches (1960) have cogently argued that increased colinearity of independent variables can lead to an increase in the goodness of fit (r^2) when data have been aggregated. This deceptive gain in the explanatory power of an aggregated independent variable prevents a direct compari-

TABLE 8.—Correlations of fishing effort (fisherman-days) (*f*) among cluster analysis species groups.

Group effort	f1	f2	f3
f1	1.000	0.943**	0.900**
f2	—	1.000	0.940**
f3	—	—	1.000

**Significant $P = 0.01$, df = 78.

son of the coefficients of determination obtained from different levels of grouping. Thus it is improper to compare the goodness of fit for the grouped analysis to that for the total aggregate without correcting for this bias. They suggest that a more appropriate and direct way of comparing the effect of these two levels is to compare the proportion of variance in the total catch explained by the predicted total catch from the two levels of aggregation. We must use catch rather than CPUE as the dependent variable because the sum of the CPUE values predicted from each of the grouped models will not predict total CPUE.

When annual catch (C) rather than CPUE is used the Schaefer model becomes

$$C = af - bf^2 + E \tag{2}$$

where a and b are constants, f is fishing effort in fisherman-days, and E is a normal random variable with mean 0 and finite variance. In the case when catch and effort are aggregated into the three species groups there will be three equations of the form of Equation (2) based on the grouped annual catch (C_i) and grouped annual effort (f_i) for $i = 1, 2, 3$. For the completely aggregated TBSM there will be a single equation of the form of Equation (2) with total annual catch (TC) and total annual effort (Tf). In all four equations the nonlinear regression coefficients a and b can be estimated with the 20 yr of annual data from 1959 to 1978. We can then use these coefficients to obtain predicted group annual catches ($\hat{C}_{ij}$) for groups $i = 1, 2, 3$ and years $j = 1, 2, ..., 20$, and the predicted total annual catches ($\widehat{TC}_j$) for years $j = 1, 2, ..., 20$ given the corresponding effort statistics.

We now have two estimates of total annual catch based on either $\widehat{TC}_j$ from the fully aggregated TBSM or $\hat{C}_{1j} + \hat{C}_{2j} + \hat{C}_{3j}$ from the three species groups regressions. We can compare these two levels of aggregation based on their accuracy in predicting TC. This is done by defining SS_g to be the sum of squares of $TC_j - \hat{C}_{1j} - \hat{C}_2 - \hat{C}_{3j}$ for $j = 1, 2, ..., 20$, or the deviations of the grouped predicted catch from the observed total, and defining $s_g^2 = SS_g/19$. Let SS_t be the sum of squares of $TC_j - \widehat{TC}_j$, $j = 1, 2, ..., 20$, or the deviations of the predicted total catch of the completely aggregated TBSM from the observed total catch. Finally let $s_t^2 = SS_t/19$ and s_{TC}^2 be the sample variance of the total annual catch. Then the proportion of the variance of the total annual catch explained by the sum of the three species groups model is r_g^2 defined as:

$$r_g^2 = 1 - s_g^2/s_{TC}^2 \tag{3}$$

and the proportion of the variance in the total annual catch explained by the TBSM is r_t^2 defined as:

$$r_t^2 = 1 - s_t^2/s_{TC}^2\ . \tag{4}$$

For the MLKM bank we determine $r_t^2 = 0.14$ and $r_g^2 = 0.18$. Thus the increased level of data aggregation going from treating the fishery as three separate groups to one total group does not in fact improve the fit of the catch curve although this appeared to be the case when the r^2 for the TBSM applied to the total group was compared to the r^2 values for the TBSM applied to each of the three cluster groups (Table 4, Fig. 4). As outlined previously these coefficients of determination, as calculated above, refer to the prediction of catch from effort data, for which the fit is substantially poorer than the fit of CPUE on effort.

A consideration of statistical aggregation theory has shown that the classification of bottom fish species into cluster groups results in slightly better predictions of total bottom fish catch than does analysis of the total aggregate. Since superior performance is achieved at an intermediate level of aggregation, it is possible to discount the undesirable effects of "averaging" which have troubled previous investigators (FAO 1978; Pauly 1979; Pope 1979). Furthermore, the lack of significant interaction among the species groups (Table 6) suggests that this particular application of the TBSM to the Hawaiian offshore handline fishery is appropriate.

Even though the separation of data from the MLKM bank into three species groups produced only a marginally better fit than the total aggregate model and the extra computations which are necessary were extensive (e.g., clustering), some advantage can be gained by splitting the fishery up into the groups listed in Table 3. Not only is the biological realism of the stock-production analysis enhanced but interesting patterns are also allowed to emerge. Notice, for example, that while the estimate of MSY for Group I from the MLKM bank is less than that for Group III from the same bank (Table 5), the fishing effort required to reach that figure is substantially greater, in spite of the fact that the catchability coefficient for Group I is greater than for Group III. This apparent contradiction can be understood when estimates of carrying capacity and instantaneous growth rate are computed for the two groups. Ricker (1975) showed that the virgin shock biomass (B_∞) is equal to a/q and the intrinsic rate of natural increase (r) is equal to aq/b, where q is the catchability coefficient and a and b are the intercept and slope, respectively, of the regression of CPUE on effort. Using these equations the estimate of virgin biomass for Group I at the bank is much less than for Group III whereas the intrinsic rate of natural increase for Group I is nearly double that of Group III, hence, the disparity in catchability coefficients. This manner of evaluating the growth dynamics of the fishery implies that if fishing were to stop abruptly, Group I would recover to pristine levels much sooner than either Group II or III. Thus, this analysis would predict that a form of succession would occur around the MLKM bank if fishing were curtailed as a new equilibrium point was approached. Although there is little hope of manipulating the system to test this particular prediction of the model, this type of heuristic calculation can provide valuable insights concerning the consequences of different management programs.

Pope (1979) has shown that in a multispecies fishery an increase in the colinearity of effort values among species or groups will result in a more parabolic-shaped yield curve. Consequently, he argues that if fishing pressure is exerted in such a way that the fishing mortalities of the various species remain in constant ratio to one another, then the use of the TBSM is a realistic management option. He points out though, that it cannot be concluded that an MSY estimated by application of the model to actual data is anywhere near the global maximum of the system. These considerations bear directly on this study because of the high correlations of fishing effort among the three species groups. Even though MSY from the MLKM bank is estimated to be 106 t/yr it is quite possible that a substantially larger yield could be sustained if it were possible to alter the ratios of fishing mortality among the species groups. This possibility is not unrealistic because these groups seem to be for the most part spatially separated. In principle then, appropriate management action could reduce fishing effort on one group while simultaneously increasing that on another, but at present it is impossible to speculate about what the global MSY of the MLKM bank might be.

One of the least realistic aspects of the TBSM is its inability to adequately model trophic dynamics (Pauly 1979). The addition of Lotka-Volterra interaction terms to the model (Pope 1979) is a relatively simplistic attempt to deal with this problem. Pauly (1979) argued that the surplus-yield of fish predator-prey systems may be overestimated by the TBSM because of "prudent predation" by top carnivores. This theory (Slobodkin 1961) would propose that fish predators optimally harvest their fish prey, leaving little or no remaining latent productivity of the prey species for man to utilize. These arguments must impose group selectionist reasoning and suffer as a result. Nevertheless, the TBSM assumes that total stock size is greatest in a virgin state, a condition which need not be satisfied if limitation is internally imposed (May et al. 1979).

Fortunately these considerations do not detract from the value of the present analysis. The six dominant species in the fishery (opakapaka, ulua, uku, onaga, hapu'upu'u, and kahala) are all high-level carnivores and occupy a similar trophic position. No predator-prey relationship is known to exist between any of the 13 species listed in Table 1, although extensive gut content analyses of all life history stages are currently unavailable. Thus, some of the objectionable aspects of the TBSM have been minimized by not including species from different trophic levels within the same analysis. Predator-prey relationships in a fisheries context are poorly understood at present and will probably require a more dynamic construct than the TBSM is capable of offering (May et al. 1979; Pauly 1979).

SUMMARY

Examining the HDFG catch report data shows that the commercial deep-sea handline fishery in the Hawaiian Islands is a multispecies fishery composed principally of 13 species of bottom fish, 6 of which comprise 86% of total landings. Snappers (Lutjanidae), jacks (Carangidae), and a species of grouper (Serranidae) dominate the catch, all of which are high-level carnivores.

In the main high islands of the Hawaiian Archipelago (see Figure 2) three bottom fish species groups are recognized based on cluster analyses which measure the tendencies of the various species to appear with one another in the catch. These groups seem to segregate on the basis of depth distribution, providing convenient biological assemblages for aggregating catch statistics.

Application of the Schaefer stock-production model to this fishery on a species-by-species basis provides an inadequate description of productivity. When species are aggregated into the cluster groups and analyzed with TBSM, the results are much improved. In this regard consistently significant results and production estimates were obtained from the MLKM bank, a region which presently accounts for half of the State of Hawaii's catch. No significant interaction among these groups was detected. When all 13 species are analyzed together, the results are in agreement with the preceding analysis. Based on TBSM applied to the MLKM bank, we estimate the annual MSY of the commercial deep-sea handline fishery to be 106 t or about 272 kg/nmi of 100-fathom isobath. Because recreational catch is unaccounted for, these figures are considered lower bounds for the gross production obtainable from this type of fishery although currently the commercial fishery is operating close to this MSY level.

By examining the effect of aggregating catch statistics we show that the production models based on the intermediate level of catch aggregation (cluster groups) together explain slightly more of the variation in the total catch than does the production model based on the total aggregate catch in spite of a higher coefficient of determination resulting from the latter analysis. High correlations of fishing effort among cluster groups account for this nonintuitive result.

Application of the Schaefer stock-production model to catch and effort data aggregated over species can be a useful tool for the analysis of a multispecies fishery. The appropriate level of aggregation will depend on biological and geographic factors.

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THE INTERNATIONAL SKIPJACK YEAR PROGRAM OF THE INTERNATIONAL COMMISSION FOR THE CONSERVATION OF ATLANTIC TUNAS

Gary T. Sakagawa and Philip E. K. Symons

ABSTRACT

A four-year research program to obtain information for assessing the condition of the Atlantic skipjack tuna, *Katsuwonus pelamis*, population and for developing plans for the rational exploitation of the resource was initiated by the International Commission for the Conservation of Atlantic Tunas (ICCAT) in 1979. The program has so far contributed to the development of a new fishery off Brazil, completed exploration of potential fishing areas in the Caribbean Sea and off Angola, sponsored tagging of 27,700 fish, and generated a considerable amount of fishery statistics and biological information. Analysis of the data and information is planned for 1982 and a scientific meeting is planned for 1983 to review the results and relate them to the needs of the ICCAT.

Gary T. Sakagawa

Philip E. K. Symons

All of the principal tuna species except the skipjack tuna, *Katsuwonus pelamis* (Fig. 1), are believed to have reached or are fast approaching full exploitation at their maximum sustainable yields. Skipjack tuna is believed to constitute a vast pelagic resource that is underutilized and is viewed as a source for new raw material to meet a growing demand, particularly for canned tuna (Matsumoto 1974). In 1979, the yield of skipjack tuna from the world's oceans was approximately 700,000 tons. It is estimated that this production can be increased by as much as 1.5 million tons if the stocks become fully exploited (Kawasaki 1973). While there has been some doubt that such a large yield is available (Kawasaki 1973), there is evidence that vast areas of the oceans where skipjack tuna occur are not currently fished except by local, small-scale fisheries, and several nations are building large tuna fleets to take advantage of this opportunity. In the Atlantic Ocean, for example, most of the fishing for skipjack tuna is conducted in the eastern part by large purse seiners and baitboats. In the western part, the fishery is less developed and involves primarily local, small boats.

Between 1969 and 1974, the skipjack tuna catch in the Atlantic increased substantially from 28,000 tons to 118,000 tons (Fig. 2), surpassing the catch of any of the other major tuna species(bluefin, yellowfin, bigeye, and albacore). Then, in 1975, it fell sharply to 61,000 tons before recovering to 118,000 tons in 1977. More recently, the catch decreased between 1977 and 1979 and increased since then, recording a record high of 139,000 tons in 1981. About 97% of the catch is from the eastern Atlantic and the skipjack average about 45 cm long.

In 1975, the International Commission for the Conservation of Atlantic Tunas (ICCAT), an organization chartered to maintain the Atlantic tuna stocks at levels permitting maximum sustainable yields, took note of the growing fleet of particularly large purse seiners and the sharp decline in catch. It immediately initiated a special investigation to determine the condition of the stocks. The investigation showed that information upon which to base an adequate assessment was not available although there was a general feeling among scientists that the stocks were not yet fully exploited (ORSTOM 1976). Consequently, the Commission's Standing Committee on Research and Statistics (SCRS) recommended in November 1976 that research be expanded to obtain information for an adequate assessment and for rational exploitation of the resource. A working group was convened in August 1977 to develop a detailed Atlantic-wide research plan for skipjack tuna. The plan (ICCAT 1978) consisted of a set of activities to be executed during a four-year period, starting in 1978, with the goal of answering four questions:

A. Can catches be increased by fishing new areas and new stocks, especially in the western Atlantic?

B. Can catches be increased by fishing larger fish, especially fish over 5 kg?

C. What could be the effects of the above increased fishing on the existing fisheries?

D. How can better assessments of the stocks be obtained by using information from the existing fisheries?

A sum of $685,000 was estimated to be required to support activities of the plan and for coordinating services of the four-year program. In addition, participating countries would provide "matching" support through contribution of vessel time, scientific personnel services, equipment, etc., for executing the activities.

A year later, after some modifications, the Commission approved the plan and budgeted $522,000 for the program to begin in 1979 (ICCAT 1978, 1979). Since then, the SCRS, through a Submcommittee on Skipjack Tuna along with the ICCAT Secretariat and scientists from several countries, has guided the

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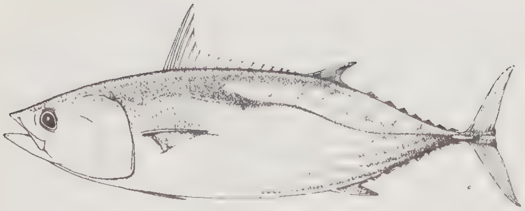

Figure 1. Skipjack tuna, *Katsuwonus pelamis*, is an underutilized resource that could fill growing demands for canned tuna. Individuals can reach a length of 80 cm long but are usually caught in the Atlantic Ocean when about 40–50 cm long.

execution of the plan.

This report describes the progress of the ICCAT International Skipjack Year Program to date and outlines program events that are to follow.

THE PROGRAM, ITS SCHEDULE AND MANAGEMENT

The International Skipjack Year Program is an ICCAT-coordinated research effort that is tailored to address the four questions mentioned above. The program relies on participating organizations to provide the bulk of the resources to execute the activities and the ICCAT Secretariat to provide coordinating services. It is not a program in which participating organizations contribute money to ICCAT which is then parceled out to individual scientists to conduct the research.

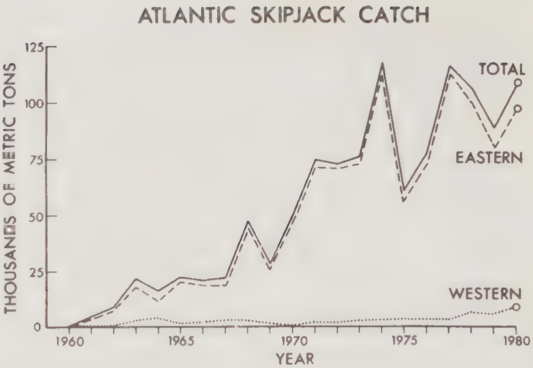

Figure 2. Skipjack tuna catches by regions of the Atlantic Ocean, 1960–1981.

Soon after the Commission approved the program in November 1978, the Secretariat recruited a full-time program coordinator. In April 1979, the coordinator entered on duty and detailed planning of research activities commenced in earnest.

A schedule for the program was first developed in 1977, but was modified in 1978. The final schedule developed for the program consists of four phases, corresponding to each of the four years 1979-1982 of the program (Fig. 3). The first phase, which was largely completed in 1979, involved detailed planning of research activities and preparations for execution of these activities. This was followed by a second phase (1980) which consisted of small-scale experiments to test research designs, and analyses of historical data for improving the designs and

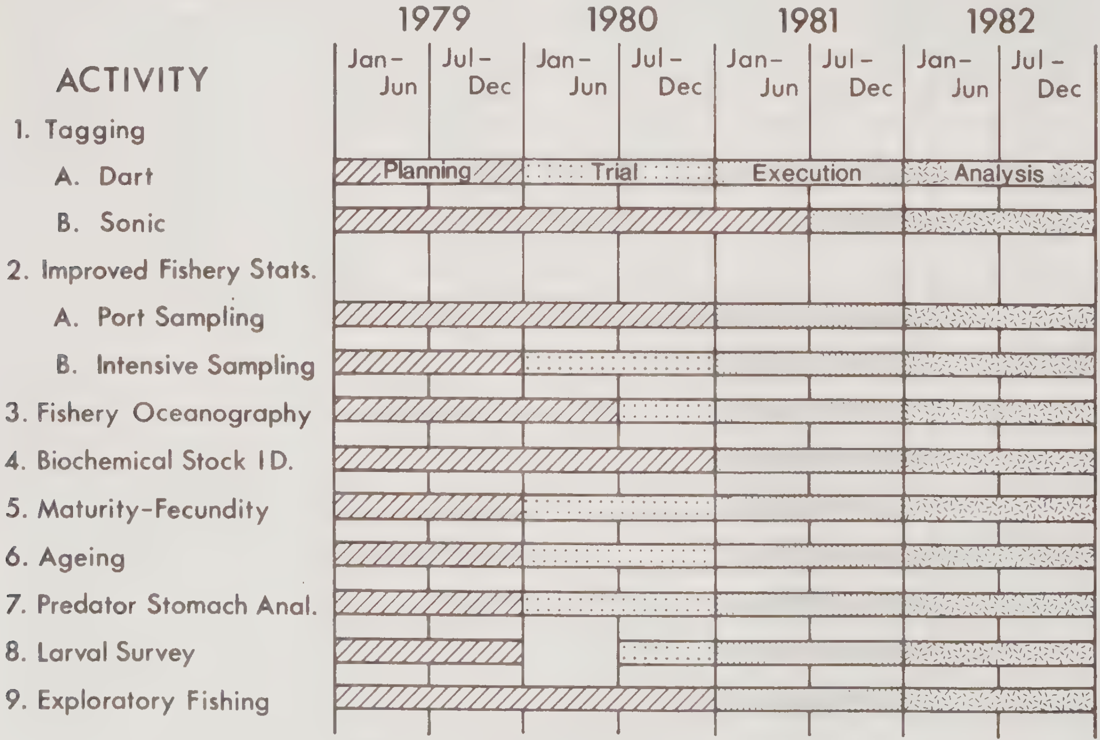

Figure 3. Schedule of planned activities of the ICCAT International Skipjack Year Program. The four phases (planning, trial, execution, and analysis of the program) are shown.

preparations for field experiments. The third phase (1981) involved the execution of all program activities. In the final phase (1982), data and information collected in 1980 and 1981 will be analyzed and evaluated. Dismantling of the program also will begin during this final phase. In 1981, the Commission approved a one-year extension of the program so that a scientific conference to discuss the results of the program can be organized for the summer of 1983.

The program is "steered" by a subcommittee composed of scientists from all participating ICCAT member countries. The current members of the ICCAT are Angola, Benin, Brazil, Canada, Cape Verde, Cuba, France, Gabon, Ghana, Ivory Coast, Japan, Korea, Morocco, Portugal, Senegal, South Africa, Spain, the United States, and the U.S.S.R. One of the scientists on the subcommittee is appointed Convener, to be responsible for calling meetings, for delegating work among members of the Subcommittee and invited scientists, and for serving as the interface between the Subcommittee and the Secretariat. In this capacity the Convener works with the Program Coordinator, a staff member of the ICCAT Secretariat who manages the day-to-day affairs of the program, and the SCRS Chairman, who oversees the scientific affairs of the ICCAT.

PROGRAM ACTIVITIES

Nine activities (Fig. 3) were identified for the program, each designed to provide information to answer the program questions. These activities may be loosely grouped according to the program questions they are designed to address.

Can New Areas Be Fished and Larger Individuals Exploited?

There are four activities aimed primarily at these questions: fishery oceanography, larval surveys, predator stomach analysis, and exploratory fishing.

THE AUTHORS: Gary T. Sakagawa is Chief of the Oceanic Fisheries Resources Division of the Southwest Fisheries Center, NMFS. He received a B.A. in zoology from the University of Hawaii, an M.S. in fisheries from the University of Michigan, and a Ph.D. in fisheries from the University of Washington. Before joining the staff of the Southwest Fisheries Center (SFWC) he worked at the Honolulu Laboratory (SWFC), the Great Lakes Fishery Laboratory under the U.S. Fish and Wildlife Service, and the Fisheries Research Institute, University of Washington. In his current position he is responsible for managing Federal research on tunas, billfishes of the eastern Pacific Ocean, dolphins involved in the eastern tropical Pacific tuna fishery, and coastal marine mammals of California. Since 1976 he has served as a member of ICCAT's Standing Committee on Research and Statistics, and since 1978 has been Convener of the Subcommittee on Skipjack Tuna. **Philip E. K. Symons** is a current Coordinator of the International Skipjack Year Program at ICCAT, responsible for the planning, execution, and analysis of activities among scientists of the 19 member countries. He received a B.S. and an M.S. in marine biology from the University of British Columbia and a Ph.D. in zoology from the University of Leiden, The Netherlands. Before joining ICCAT, he served on the staff of the Canadian Department of Fisheries and Oceans, first at the St. Andrews Biological Station and later at the Pacific Biological Station.

Fishery oceanography has two objectives: (1) To investigate the relation between environmental factors (such as temperature, oxygen concentration, sea state) and fishing success. Weather and oceanographic data from many sources—including satellites, oceanographic and merchant vessels, and fishing vessels—are to be collected and analyzed with data on fishing success kept by fishermen or technicians aboard fishing vessels. (2) To identify areas of the Atlantic Ocean where skipjack tuna might occur, but where fisheries are not currently present or developed. Skipjack tuna is primarily a tropical species having broad habitat requirements. Analysis of environmental data on habitat requirements of skipjack tuna will be used to identify areas for development of new fisheries.

Larval surveys are to be conducted to identify new spawning areas where large, adult skipjack tuna may be present. These new areas may be suitable for developing new fisheries.

Analysis of the stomachs of large predators, particularly billfishes (Istiophorids), for the presence of juvenile skipjack tuna provide information on the distribution of juveniles, and more importantly, the possible presence of adult skipjack tuna (Yoshida 1971). This too is another means of identifying new areas where adult skipjack may be available for fishery development.

Activities of fishery oceanography, larval surveys, and predator stomach analysis provide information on where exploratory fishing can be most profitably performed. Exploratory fishing in new areas should provide information on the presence or absence of skipjack tuna and also their abundance in quantities for commercial fishing development (Fig. 4). For this purpose, carefully collected statistics and biological samples are part of the program plan.

Will New Fisheries Affect Existing Fisheries?

Recurrent questions for the management of any fishery are "how many breeding populations make up the exploited stock, and what is the degree of exchange between these populations?" If an exploited stock is composed of separate breeding populations, management strategies may have to be devised for each population individually to obtain desired yields while preventing overfishing or underutilizing one or more populations.

The contribution of larval surveys and predator stomach analyses to the location of spawning grounds and the determination of spawning stock separation has already been mentioned. Other activities which contribute directly to this knowledge are tagging and biochemical stock identification.

The tagging activity consists of two parts: (1) tagging with dart tags and (2) tagging with sonic tags. Dart tags consist of individually numbered spaghetti-shaped, 15-cm lengths of plastic with a barb-like point of hard plastic at one end (Yamashita and Waldron 1958). The point is inserted and anchored in the dorsal muscle of the skipjack in an operation that ideally keeps the live fish out of water no longer than 5 to 7 seconds. From the release and recovery of such tagged fish, information is obtained on movement, age and growth, survival and exploitation rates.

Sonic tags emit an ultrasonic signal that may be coded for transmittal of data, such as depth and temperature. The battery-powered signal is detectable with hydrophones over distances usually less than one kilometer and over a period of several days. The released fish is tracked closely by boat during this period. This activity is designed to investigate the daily movements of skipjack tuna and patterns of swimming behavior (Yuen 1970). This information is important to studies of migration and availability of skipjack tuna to the fisheries.

Biochemical stock identification is an activity that compares the frequency of occurrence of certain proteins among skipjack

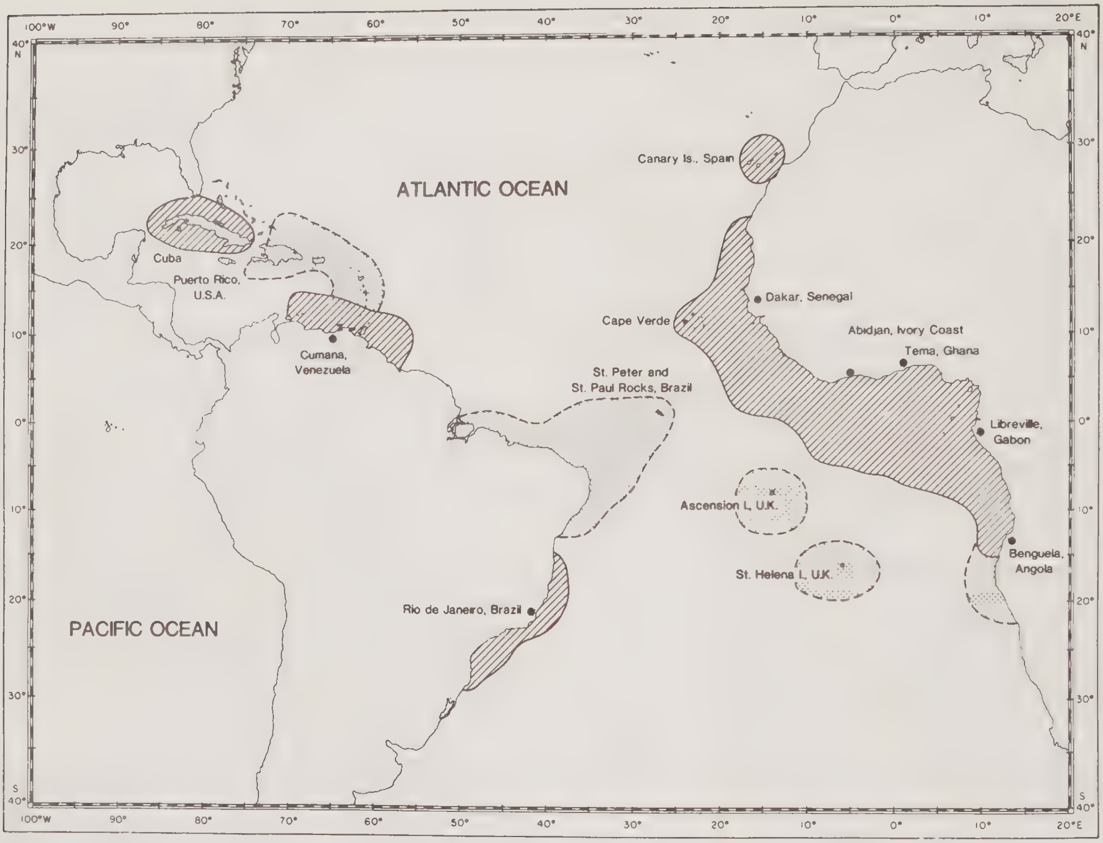

Figure 4. Areas of the Atlantic Ocean where current fisheries for skipjack exist *(hatched)* and where exploratory fishing is suggested *(stippled).*

tuna of a group caught at one location with the frequency of these proteins in another group caught at the same or another location (Fujino 1970). If the frequencies are sufficiently different between the two groups, they may be from diffierent genetic populations. The sampling design and statistical analysis of data for this activity are complex, but a modest effort will be made to use this tool to detect differences between eastern and western Atlantic skipjack tuna.

How Can Assessments of Stock Condition Be Improved?

There are three activities that are directed primarily at answering this question: a study of maturity-fecundity, age determination, and an activity aimed at improving the collection of fishery statistics. One principle of fishery management is to maintain the spawning stock at a level sufficient to produce young to replace losses from fishing and natural causes. Size, age at maturity, sex ratio, and number of eggs produced by a mature female are types of information that contribute to determining the condition of the spawning stock. These data will be assembled from the maturity-fecundity activity.

Because skipjack tuna is a tropical species, individuals do not show typical annuli on scales or other hard parts as found in individuals of more temperate species. Fine rings on otoliths and bands on dorsal fin spines of skipjack tuna have been reported and used for aging with limited success (Batts 1972; Wild and Foreman 1980). A special study will be initiated with tagged and tetracycline-injected fish to determine timing of formation of rings on otoliths and bands on dorsal fin spines for aging purposes.

Besides the need to determine age and fecundity of skipjack tuna, there is also the need to determine just how much fishing effort is expended annually to catch skipjack tuna, how many fish are caught, and where they are caught. These data are indispensable for developing models from which to assess the effects of exploitation on each population. Currently, catch and fishing effort statistics for skipjack tuna are incomplete, and fishing effort statistics are intermeshed with statistics for yellowfin tuna, *Thunnus albacares*, because the tuna fleets search and catch both species simultaneously (Sakagawa, Coan and Murphy 1977). To resolve this situation, two sub-activities for improving statistics have been devised: increased or improved "port sampling" and "intensive sampling" of vessels.

The port sampling activity has been designed to collect fishery data at every major skipjack tuna landing port in the Atlantic. The catches, the sizes of fish in the catches, and the time spent by vessels in searching and catching skipjack tuna will be measured. This information will be used in stock assessment models as well as in determining the levels of port sampling coverage that is necessary to monitor the fishery accurately on a routine basis.

Intensive sampling, in contrast, is designed to collect fishing operations data aboard purse seiners and baitboats during a short period and within a small fishing area of the eastern Atlantic. These data will be used to study the performance of the different fleets, procedures for accurately measuring fishing effort on skipjack, and the relationships between abundance, catch-per-unit of effort, fishing effort, and fishing mortality. Collectively, this information will contribute to improving ICCAT's ability to assess more accurately the condition of the skipjack tuna stocks.

THE PRIMARY ACTIVITIES

Of the nine planned activities (Fig. 3), three are of primary importance to the program because they provide a focus for field collection of data and information upon which the other activities depend.

These primary activities are exploratory fishing, tagging, and improved statistics. Vessels used in exploratory fishing, tagging, and intensive sampling can be used to collect fishery oceanography and fishing operations data, gonad samples for the maturity-fecundity activity, blood samples for the biochemical stock identification activity, plankton tows for larval fish examination, and samples of stomachs from large pelagic species for the predator stomach analysis activity. Samples of gonads and stomachs, and tag return information can be collected by persons sampling catches at landing ports.

ACCOMPLISHMENTS IN 1979, 1980, and 1981

Detailed planning of activities and analysis of historical data were completed in 1979. Field trials were performed in 1980 and all activities were executed in 1981, the International Skipjack Year. Complete results on the activities are not yet in and analyses of data and information collected are currently underway; however, the program has already yielded some noteworthy accomplishments, particularly from the primary activities.

Exploratory Fishing

Exploratory fishing is an activity with unique political and industrial sensitivities. Discoverers of new fishing areas naturally feel they should have first rights to the fruits of their investments. If this new fishing area should be within the territorial waters or fisheries conservation zones of foreign nations, the importance of politics is obvious. Moreover, skipjack tuna are migratory and development of new fishing areas can influence fishing performance elsewhere. While this migratory habit of skipjack favors—indeed necessitates—international cooperation for the management of the resource, the nature of exploratory fishing itself tends to favor private undertakings. The role of the ICCAT in this activity, therefore, has been important but limited.

The Commission has functioned thus far as a center for dissemination of plans and information on where and how exploratory fishing should best be carried out. During the planning phase, several areas for skipjack tuna exploration were identified from existing data on larval distribution, catches of local fisheries, performance of past exploratory cruises, and oceanography (Evans, McLain and Bauer 1981). Included in the list was the area off Rio de Janeiro, Brazil (Fig. 4): exploration occurred here in 1978 and 1979 and a new and growing fishery (catch of 20,000 tons in 1981) has developed since then. Other areas identified for exploratory fishing include the Caribbean Sea, an area off the northeast tip of Brazil to the islands of St. Peter and St. Paul Rocks in the western Atlantic, and waters off Angola, St. Helena Island, and Ascension Island in the eastern Atlantic (Fig. 4).

In 1980 and 1981, exploratory fishing cruises were conducted in the Caribbean Sea and off Angola. One cruise (U.S.A.) during February through April 1980 explored the region of the Caribbean Sea from the Dominican Republic to the coast of Surinam (Rinaldo, Evans and Vergne 1980). In 54 days of fishing operations, 143 fish schools were sighted. Skipjack tuna was the primary species in 38% (54 schools) of these schools. Most of the schools consisted of tuna and were 10–20 tons in size.

Nine exploratory fishing cruises (Cuba) were executed off the southeastern coast of Cuba during May to August 1981. Skipjack tuna was found to be low in abundance and of sizes less than 30 cm long (ICCAT 1981).

An exploratory cruise (U.S.S.R) was conducted off Angola in 1980. Only 11 schools of skipjack tuna were sighted during that cruise.

Tagging

An ambitious activity of tagging skipjack tuna with dart tags was conceived for the program, with plans to single- and double-tag as many as 30,000 skipjack tuna in 1980, and 50,000 in 1981 in both the western and eastern Atlantic. The plans also called for as many as 35,000 of the tagged fish to be injected with tetracycline to investigate the rate of deposition of growth rings on spines and otoliths for age determination studies.

To encourage return of recovered tags, ICCAT established awards of $4.00 or a T-shirt (with the emblem of the International Skipjack Year Program) per tag and two $500 annual lotteries. One lottery is for returns from the western Atlantic and the other for returns from the eastern Atlantic.

In 1980, approximately 9,200 fish were tagged, including about 6,000 skipjack tuna by a charted commercial baitboat (Japan) working in the Gulf of Guinea and 1,400 skipjack tuna by a chartered commercial baitboat (U.S.A.) working in the Caribbean Sea. The remainder were released in the eastern Atlantic by commercial vessels (Korea and Spain) on an opportunistic basis and by research vessels (France) temporarily modified for fishing and tagging of skipjack tuna.

While these 1980 efforts did not result in the desired number of tag releases, they were important in providing participating scientists an opportunity to test and perfect their tagging procedures and to conduct ancillary research, particularly research involving collection of biological samples.

In 1981, scientists from nine countries participated in tagging of approximately 18,500 skipjack tuna. All except about 600 fish were tagged in the eastern Atlantic. Major release sites were the Gulf of Guinea, 12,200 fish (Japan and Ivory Coast); around Cape Verde Islands, 2,700 fish (Cape Verde); off Senegal, 2,500 fish (Senegal); around the Canary Islands, 700 fish (Spain); and off Cuba, 600 fish (Cuba).

Tag returns of skipjack tuna released in 1980 and 1981 are being received by ICCAT and are expected to continue through 1983. So far the results show that (1) the recovery rate is variable, from 0 to 18%; (2) most of the tags are recovered in the general area of release; and (3) a few long-distance recoveries within a year of release have been reported. Noteworthy among these is a skipjack that was tagged in the Canary Islands and recaptured off Senegal, a distance of approximately 1,700 km, and five skipjack that were tagged off Ghana and recaptured off Senegal, a distance of approximately 2,800 km.

Lotteries for tags returned in 1980 were held in March 1981, with a winner from the United States and a winner from the Ivory Coast. Lotteries for 1981 returns are scheduled for 1982.

Improved Statistics

Getting this activity underway required two concerted actions: (1) arranging for the placement of trained technicians at landing ports (Port Sampling) and aboard vessels (Intensive Sampling) and (2) preparing detailed instruction manuals for the sampling work so that data are comprehensive and collected in a standardized manner.

Of the 19 member countries of the ICCAT, 17 fish for skipjack tuna, although the landings by local (artisanal) fisheries in some of these countries appear to be small. In addition, there are several non-member countries, particularly in and around the Caribbean Sea, whose artisanal fisheries land some skipjack and where, in at least one country, catches may be landed or transshipped by foreign vessels in quantity. Most member countries planned to sample landings at their major ports at least through 1981, and most were able to mount substantial effort, sometimes in cooperation with another country or with the financial assistance of the ICCAT.

Plans for intensive sampling called for placement of trained observers aboard purse seiners and baitboats fishing in the Annobon area (Gulf of Guinea) during July and August and in the Cape Verde Islands area during August through October in order to collect detailed data on searching and fishing operations and on the catches. For 1980, each member country was asked to place one observer aboard at least one vessel to obtain experience and to polish data collection procedures. For 1981, the year of maximum effort, nine member countries were asked to place observers on 20–25% of their vessels that fish in the experimental areas.

France and Spain were able to place an observer on one purse seiner each in 1980. Japan also placed an observer on a baitboat in 1980. Other countries had difficulty in funding this activity or had difficulty obtaining cooperation from their tuna fishing industries. Because it was evident that this situation would not improve in 1981, plans were scaled down to one experimental area, Annobon, for 1981.

In 1981, data were collected by scientists from France, Senegal, and the Ivory Coast on eight purse seine cruises, Spanish scientists on five purse seine cruises, and Japanese scientists on two baitboat cruises. Data collected on these cruises are being prepared for analyses and are proving to be useful in understanding the searching behavior of the vessels. However, because the number of vessels observed was less than planned, these data probably will not be adequate for performing planned analyses with the same confidence as was hoped.

EVENTS TO FOLLOW

The concept of an International Skipjack Year Program was formulated to encourage a concerted research effort by all interested ICCAT member countries by pooling their resources and performing their research in an integrated manner. In this way, the countries would avoid the costs of extended piecemeal research projects and unnecessary duplication of effort. While the field work for the program officially terminated at the end of 1981 and the program ends officially in December 1983, some field work is continuing into 1982 and improved procedures for data collection are being retained in routine fishery monitoring activities of member countries.

Analysis of data collected in 1980 and 1981 is currently underway and will probably continue for several years after the official termination of the program. A scientific conference is scheduled tentatively for 1983, when the results from the program will be reviewed and related to general stock assessment needs of the ICCAT.

One peripheral issue in ICCAT that will benefit from results of the program is that of appropriate regulations for protecting juvenile tunas from capture in multi-species fisheries while maintaining optimum yield-per-recruit. ICCAT currently has a minimum-size regulation of 3.2 kg (approximately 55 cm) for yellowfin tuna and bigeye tuna, *Thunnus obesus*. Because undersized bigeye and yellowfin tunas often occur in mixed schools with skipjack tuna, fishermen have claimed that the regulation discourages full utilization of the skipjack resource and is not having the desired effect. Mixed schools must either be avoided, or, if fished, the undersized bigeye and yellowfin tunas must be discarded, usually dead. This results in economic loss to the fishermen and loss in potential yield from the bigeye and yellowfin tuna stocks. Attempts have been made to develop models showing how catches would be altered under different sets of alternative regulations, but these have concluded that information was insufficient for proper evaluation of alternatives. When results from the Skipjack Program have been processed, further analyses can be performed to find a solution to this complex, practical problem.

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DETERMINACION DEL ESFUERZO DE MUESTREO REQUERIDO PARA EL ESTIMADO DE PRODUCCION DE HUEVOS DE ANCHOVETA, *Engraulis ringens*, FRENTE AL PERU

Haydeé Santander[1], Paul E. Smith[2] y Juergen Alheit[3]

1 Instituto del Mar del Perú, Apartado 22, Callao, Perú
2 NOAA, National Marine Fisheries Service, Southwest Fisheries Center, P. O. Box 271, La Jolla, California 92038, U.S.A.
3 Programa Cooperativo Peruano-Alemán de Investigación Pesquera (PROCOPA)
Instituto del Mar del Perú, Apartado 22, Callao, Perú.

RESUMEN

Para obtener una primera aproximación del número de muestras requerido para un determinado nivel de precisión del estimado de producción de huevos de anchoveta por unidad de área superficial del mar, se han utilizado datos existentes de muestras de huevos provenientes de exploraciones efectuadas frente al Perú en los últimos 20 años. La anchoveta parece desovar en cardúmenes, produciendo una gran cantidad de huevos, de los que las muestras toman una pequeña proporción. Aproximadamente el 8°/o de las muestras positivas fueron superiores a 4096 huevos por m^2. Un importante cambio en el tamaño de la población de la anchoveta peruana se ha notado en 1972. El rango de valores de huevos fue similar antes y después del cambio, pero el número promedio de huevos por muestra positiva fue aproximadamente el doble antes de la declinación en 1971.

Se ha tomado en consideración la precisión de la estimación deseada y los costos y disponibilidad de tiempo de barco en la estación de desove para elaborar un plan de crucero a un costo razonable. El área investigada cubre 57600 millas cuadradas; con 640 millas a lo largo y 90 millas hacia afuera de la costa. En esta proyección una precisión del estimado de 30°/o requiere 924 muestras y 20°/o de precisión requiere 2078 muestras. Se discute los sesgos en la estimación de precisión. Se usa la distribución de probabilidad log-normal en la descripción de muestras positivas.

INTRODUCCION

Es muy difícil estimar la biomasa de peces distribuídos ampliamente en el mar pero a menudo es necesario hacerlo cuando se trata del manejo de las pesquerías y de prevenir la sobrepesca no deseada. En el siglo 20, el desarrollo de la metodología adecuada para estimar biomasa ha ido paralela al crecimiento de la pesca mecanizada.

Los métodos indirectos incluyen análisis de captura y exploraciones acústicas. Los métodos directos consideran los muestreos cuantitativos de peces adultos y las exploraciones de desoves. En las exploraciones de producción del desove se usan datos de fecundidad, abundancia de huevos o larvas y mortalidad de huevos o larvas para calcular la biomasa desovante a base de la producción de huevos encontrada en el agua.

Tanto los métodos directos como los indirectos ofrecen dificultades referentes a costos, baja precisión causada por la baja ocurrencia de los organismos, y el tiempo transcurrido entre el estimado del tamaño del stock y la implementación de los controles de la pesca.

Recientemente ha sido desarrollado (Parker, 1980) y aplicado (Stauffer and Picquelle, 1980) un método directo e instantáneo para estimar la biomasa desovante de la anchoveta de California, *Engraulis mordax*, que minimiza las desventajas enumeradas.

Las investigaciones de desove para estimados de biomasa de desovadores múltiples, tales como la anchoveta de California, fueron limitados por la falta de información del número de desoves por año. Este problema ha sido resuelto para esta anchoveta por los estudios de Hunter and Goldberg (1979), Hunter and Macewicz (1980) y Hunter and Leong (1981) que revelaron que ésta especie desova aproximadamente 20 veces al año. Hay evidencia que también ésto es aplicable a la anchoveta peruana, *E. ringens* (Santander, Alheit y Smith, Manuscrito).

El nuevo método se denomina "Método de Producción de Huevos" (Stauffer and Picquelle, 1980) debido a que el estimado de la biomasa es derivado de los estimados de producción de huevos en el área de desove y de la tasa de producción de huevos por unidad de biomasa de la porción de adultos del stock.

La producción de huevos en el área de desove es inherentemente el parámetro más variable de este método. Las causas fundamentales para ésto son: (1) los huevos son desovados por agregaciones densas de peces adultos, (2) los peces desovan durante más o menos la mitad de cada día, (3) los huevos están sujetos a una alta tasa de mortalidad la que puede ser muy variable. Los otros parámetros son:

- el número de huevos producidos en una noche por unidad de peso de hembra adulta,
- la fracción de hembras que desova cada noche, y
- la fracción del stock de hembras adultas en peso.

El propósito de este trabajo está limitado al estimado de la producción de huevos en el área de desove de la anchoveta peruana.

En la primera aplicación del método de producción de huevos (Parker, 1980), la contribución a la varianza en el estimado de huevos producidos por unidad de área por día fue 8 veces mayor que todos los otros parámetros combinados. El muestreo adicional en la segunda aplicación (Stauffer and Picquelle, 1980) redujo la variabilidad al mismo nivel de precisión de los parámetros derivados de la evaluación de la tasa de adultos desovantes. En este trabajo ha sido usada la distribución estadística de muestras de huevos de anchoveta (Santander y S. de Castillo, 1979) para hacer una primera aproximación del número de muestras de huevos que se requiere para estimar la tasa de producción de huevos de anchoveta con diferentes niveles de precisión. El objetivo final es encontrar el tamaño de muestra conveniente en el estimado de biomasa desovante de la anchoveta peruana en 1981.

Estas investigaciones son parte del proyecto peruano-alemán para pesquerías financiado por la Sociedad Alemana de Cooperación Técnica (GTZ).

METODOS

Mediante los resultados de un crucero con 59 muestras de huevos de anchoveta colectadas en 1961 se muestran los métodos de análisis estadístico para la primera estimación del número requerido de muestras. La distribución geográfica y estadística de estas muestras de huevos ha sido reportada por Einarsson, Rojas de Mendiola y Santander (1966).

El primer paso es ordenar los valores de huevos de las muestras, desde el más bajo hasta el más alto número por muestra. Puesto que cada muestra es 1/59 ó la 0.01695ava parte del conjunto de muestras, la frecuencia acumulada es incrementada por esta fracción para cada muestra superior, sucesivamente. El valor de cada muestra es transformada a logaritmo natural (Tabla 1). En la Figura 1 se muestra que el ploteo de la probabilidad acumulada de las muestras contra el logaritmo natural del número de huevos por m^2 es aparentemente lineal. Como un supuesto simplificante, se asume que la tendencia linear de esta muestra pequeña describe la distribución fundamental de muestras para todas las áreas de desove de anchoveta, en todo momento.

Para simplificar este análisis algo laborioso se puede agrupar los valores de las muestras. Por ejemplo, los valores de las muestras de la Tabla 1 y Figura 1 han sido agrupados en 1-4, 4-16, 16-64, etc. huevos por muestra en la Tabla 2. También se incluye el logaritmo natural del punto extremo de cada clase, la proporción de la clase y la proporción acumulativa. En la Figura 2 se plotea cada valor como en la Figura 1. Puesto que ambas líneas cortan la línea de probabilidad de 50o/o aproximadamente en el mismo punto, el procedimiento del agrupamiento puede ser considerado no sesgado para este propósito. Y desde que ambas líneas tienen aproximadamente la misma pendiente, el procedimiento de agrupamiento parece reflejar bastante bien la varianza de la distribución de la muestra total original. Puesto que este procedimiento es satisfactorio para este propósito, los subsecuentes grupos grandes de muestras obtenidos de Santander y S. de Castillo (1979) son agrupados de manera idéntica.

Entre 1966 y 1979, 911 muestras contenían huevos de anchoveta, de un total de 4028 muestras colectadas durante los cruceros de IMARPE (principalmente operaciones EUREKA) en el área de desove de anchoveta. Las muestras fueron colectadas durante diferentes meses. La Figura 3 muestra el área muestreada y la distribución geográfica de muestras de huevos, antes y después de 1971. En la Tabla 3 se dan los valores mayores colectados entre 1966 y 1979. Arbitrariamente se consideran como mayores los valores iguales o mayores que 4096 huevos por m^2. La importancia de estos valores grandes es que constituyen una gran proporción de huevos en las muestras y contribuyen a la varianza. Futuras exploraciones deben tomar un número suficiente de muestras para obtener cantidades representativas de estas muestras, para que sean precisas. El error estándar del promedio de muestras grandes es 1998 o aproximadamente 14o/o de la categoría promedio. Smith (1973) concluyó que las muestras grandes de huevos ocurren porque los tamaños de los cardúmenes se distribuyen como un mosaico y que las muestras más pequeñas se deben a la subsecuente dispersión aleatoria de los huevos en el perímetro. El rango del tamaño de las muestras incluye una muestra de 107376 huevos por m^2 y 78 muestras fueron mayores a 4096 huevos por m^2. Este rango extremo de la densidad de población de huevos ha sido notado también en otros cardúmenes de peces como la sardina del Pacífico, *Sardinops caerulea*, frente a California (Smith, 1973) y la anchoveta de California (Smith, 1981; Smith and Richardson, 1977).

Las muestras fueron colectadas con la red Hensen, la que fue usada verticalmente de 50 metros a la superficie (Santander y S. de Castillo, 1979). Dos posibles fuentes de subestimación de este muestreo son: primero, que la distribución vertical de algunos huevos de anchoveta pueda alcanzar mayor profundidad que la colectada; y segundo, que el filtrado de agua pueda ser menor que el que supuestamente corresponde a la velocidad de arrastre de la red. Dos posibles fuentes de sobreestimación son cuando la red puede estar operando oblicuamente cerca a la superficie y cuando la red puede filtrar más agua que la estimada debido a la forma de cono invertido del equipo (Tranter and Smith, 1968). Para el propósito de este trabajo se asume 100o/o de filtración y que las colecciones son perfectamente verticales. El efecto de la variabilidad originada por estas fuentes será sobreestimar moderadamente el número de muestras requerido para un determinado grado de precisión del estimado de producción de huevos. Debido a que el rango de número de huevos por muestra fue similar antes y después del cambio en la población de la anchoveta peruana, estas muestras han sido combinadas (Fig. 4). El número de muestras con valores de huevos mayores fue moderadamente mayor antes de 1971. Además el número de muestras después de 1972 fue incrementado. Las muestras sin huevos de anchoveta han sido omitidas debido a que la extensión del área de desove experimentó un fuerte decrecimiento en 1971, mientras que la cobertura geográfica de las exploraciones EUREKA en general no ha variado. El efecto de no incorporar las muestras cero es disminuir la varianza y subestimar el número de muestras requerido para una precisión dada.

El "Método de Producción de Huevos" usa la intersección en cero de una curva de mortalidad exponencial de huevos con edad determinada para estimar la producción de huevos. Los datos de distribución probable de huevos usados para estimar el número de muestras provienen de cruceros y operaciones EUREKA y considera huevos de anchoveta de todas las edades en conjunto. Puesto que en una muestra pueden presentarse huevos de tres días de desove, ésto puede hacer decrecer la varianza y subestimar moderadamente el número de muestras requerido. En las muestras propuestas para 1981 la distribución de huevos por edad dentro de cada muestra puede ser parcialmente independiente, resultando en una sobreestimación del número de muestras requerido.

RESULTADOS

La distribución de frecuencias de 911 muestras de huevos de la anchoveta peruana (Tabla 4) presenta las mismas características importantes de las muestras de huevos de la sardina y de la anchoveta de California (Smith and Richardson, 1977; Tabla 3, 10). La Tabla 4 muestra la distribución de frecuencia para los períodos anterior y posterior a 1971. Debido al amplio rango de densidades de huevos en el mar, la tabla está arreglada en grupos geométricos con categorías cuyo rango crece por un factor de 4 (1-4; 4-16; 16-64, etc.). El promedio geométrico es el valor representativo de cada categoría incrementada geométricamente. Por ejemplo, la categoría con 4 a 16 huevos por m^2 es representada por el promedio geométrico "8", en lugar del promedio aritmético "10" (Smith and Richardson, 1977). La categoría más grande es representada por el promedio de todos los valores, iguales o mayores que 4096 huevos por m^2 (Ver Tabla 3). Como el número de muestras en la categoría geométrica grande es pequeño pero importante, se ha usado un estimado no sesgado de su categoría en lugar del promedio geométrico el que puede ser sesgado.

La Tabla 5 muestra las probabilidades de la distribución de muestras de huevos. Debido a que la población de la anchoveta peruana experimentó un cambio drástico en 1971 y relativamente de largo plazo, la distribución de valores ha sido dividida en este punto. El rango de los valores de las muestras es casi el mismo para los dos períodos pero el número promedio de huevos por muestra positiva declinó de un valor medio estimado de 2645 huevos por m^2 de área superficial del mar a un valor de 1434 huevos por m^2, un factor de casi dos. La desviación estándar de ambos grupos es aproximadamente el doble del valor del promedio en ambos casos. En las Figuras 5 y 6 se muestran los ploteos de la probabilidad acumulativa de las muestras versus el logaritmo natural del número de huevos por m^2. Debido a estas similaridades, para determinar un primer estimado del número de muestras requerido para una evaluación precisa de biomasa de la anchoveta, las dos distribuciones fueron combinadas en la Tabla 6. Los parámetros de la distribución son 2038.5 para el promedio y 4425.4 para la desviación estándar.

Un estimado de los parámetros para la densidad de huevos de la población de anchoveta determina en parte los límites de confidencia del número de huevos producido por unidad de área por noche. Para estimar los límites de confidencia antes de la investigación, ha sido aplicado la técnica de la distribución t de Student para estimar los límites de confidencia de la población promedio cuando son conocidos solamente el promedio de una muestra y la desviación estándar de la muestra. La ecuación es tomada de Dixon and Massey (1957; p. 127-128):

$$\bar{X} + \frac{t_{\frac{1}{2}\alpha}\; s}{\sqrt{N}} > \mu > \bar{X} + \frac{t_{1-\frac{1}{2}\alpha}\; s}{\sqrt{N}}$$

Donde: μ es el promedio aritmético de la población.

$\bar{X}$ es el promedio aritmético (2038.5) de la muestra

t es el factor del límite de confidencia para N - 1 grados de libertad y α la probabilidad de estar en error (fuera de los límites de confidencia)

s es la desviación estándar de la muestra (4425.4)

N es el número de muestras (911)

Estos valores son fijados para los parámetros de los datos: promedio, desviación estándar y número de muestras. Para propósitos de planeamiento, los valores de α y t deben ser fijados y luego puede ser calculado N.

El valor de α es la probabilidad aceptable de estar en error en el estimado. Frecuentemente, el término usado "límites de confidencia del 95o/o" es equivalente a un α de 0.05. En este caso los límites de confidencia calculados contienen 19 de cada 20 estimados. El valor de t es una función del tamaño de la muestra N y del valor de α. Para $\alpha = 0.05$ y un tamaño de muestra mayor o igual a 60, t = 2.00. A medida que el número de la muestra crece, t se aproxima a 1.96. Por lo tanto, es conveniente usar t con un valor de 2.

El número de muestras requerido puede ser determinado también para cualquier fracción del promedio. Por ejemplo, si se decide que el promedio de la muestra debiera variar menos del 20o/o por debajo o por encima del promedio de la población, el número de muestras requerido es dado por:

$$N = \left(\frac{t_{\frac{1}{2}\alpha}\; s}{s.e.}\right)^2$$

Donde la notación es como la ya señalada, excepto que s. e. significa el error estándar del promedio. La ecuación puede ser reescrita:

$$N = \left(\frac{t_{1\ 2\alpha}\, s}{0.2\,\bar{X}}\right)^2$$

Así, con los valores t = 2 para cualquier N > 60, s = 4425.4 (Tabla 6) para colecciones verticales de huevos de anchoveta y $\bar{X} = 2038.5$ la ecuación es:

$$N = \left(\frac{2 \times 4425.4}{0.2 \times 2038.5}\right)^2 = 471$$

Cuando el error aceptable por encima o por debajo del promedio varía de 30o/o a 5o/o, se obtienen los siguientes valores para el número de muestras positivas requeridas (Promedio de muestras positivas, que contienen huevos de anchoveta):

(1) Para = 0.3	N Pos = 209	N total = 924
(2) Para = 0.2	N Pos = 471	N total = 2082
(3) Para = 0.1	N Pos = 1885	N total = 8332
(4) Para = 0.05	N Pos = 7541	N total = 33331

Como el número de muestras positivas de huevos, N Pos. es 22.62o/o del número total de muestras de huevos, N total, en la serie de datos de Santander y S. de Castillo (1979), asumiendo que el área de desove es consistente, N Pos tiene que ser multiplicado por 4.42 pra obtener el número total de muestras, N total, requerido.

DISCUSION

El "Método de Producción de Huevos" es una técnica para obtener estimados absolutos de la biomasa desovante de la anchoveta peruana. Los datos de la anchoveta de California, multidesovadora, pueden ser usados con la distribución de probabilidad espacial y temporal de las muestras de huevos de la anchoveta peruana para establecer un primer estimado del esfuerzo de muestreo requerido para una precisión dada de la tasa de producción de huevos. Esta tasa de producción de huevos integrada sobre el espacio, puede ser combinada con la producción de huevos por tonelada de peces adultos para producir un estimado absoluto e instantáneo de la biomasa desovante de la anchoveta peruana. El primer estimado de biomasa y las medidas de precisión asociadas permitirán también un afinamiento de los modelos estadísticos de precisión. Las medidas de precisión relevantes permitirán balancear el esfuerzo técnico en (1) la estimación de la producción de huevos en el área de desove y (2) de la producción de huevos por unidad de biomasa para alcanzar la más alta eficiencia técnica. El esfuerzo que se aplique en el estimado de producción de huevos en el mar también puede ser incrementado o disminuído dependiendo de los requerimientos de las autoridades responsables en el manejo de la anchoveta y de los fondos disponibles para la conducción de los estimados de biomasa.

Un resultado del método de producción de huevos es subdividir las muestras de huevos por estadíos de desarrollo y edad desde el desove. Estimados preliminares han demostrado que la disminución simultánea del número promedio de huevos por estadío y la variación en el número de huevos resulta en un estimado del número requerido de muestras comparable al obtenido del número de huevos en conjunto.

El examen de los datos de huevos colectados con la red Hensen ha sido usado para preparar un estimado preliminar del número de muestras requerido para obtener una precisión dada. Los resultados de este trabajo son mostrados en la Figura 7. La cual ilustra el hecho que el incremento de precisión requiere muchas muestras más. A condición de que las muestras sean independientes, la precisión mejora por un factor de dos, con cada aumento en el esfuerzo de muestreo por un factor de cuatro.

El plan de crucero para estimar la biomasa desovante de *E. ringens* por la producción de huevos depende de varios factores, incluyendo la precisión requerida, la extensión del área investigada cubierta por el desove de anchoveta y el número relativo de perfiles y estaciones por perfil. Para el propósito de planeamiento se han determinado tres niveles de precisión de muestreo (Tabla 7, columna 1), basados en los resultados de las muestras colectadas con red Hensen (Tabla 4, 5, 6). El área a investigarse según el plan se extiende 640 millas a lo largo de la línea costera peruana y 90 millas en distancia de la costa y cubre así 57600 millas náuticas cuadradas. Si la precisión seleccionada es ± 30o/o (Tabla 7, columna 1) se requieren 209 muestras positivas (columna 2). Si como en la serie de muestras usada aquí, la proporción de estaciones positivas es 22.62o/o, el número total de muestras requerido es 924 (columna 2). Con un área total de investigación de 57600 millas cuadradas, se requeriría entonces que cada muestra represente 64 millas cuadradas. Esto se efectuaría subdividiendo el área de investigación en cuadrados; en este caso en cuadrados de 8 x 8 millas cuadradas (columna 3). Las muestras que representan una unidad cuadrada de área tienen algún mérito. Sin embargo, como la unidad cuadrada requiere el máximo de recorrido del barco y de tiempo, se exploran otras opciones. Frecuentemente, los perfiles costeros son espaciados con mayor distancia para reducir tiempo de recorrido de barco. Si las estaciones estuvieran a 4 millas de distancia, los perfiles podrían estar espaciados 16 millas (columna 3) para mantener igual densidad. El número de perfiles en la sección costera de 640 millas sería reducido de 80 a 40 (columna 4); ésto significaría una reducción del costo de recorrido de barco de los perfiles de 7200 millas a 3600 millas (columna 5), una reducción de 50o/o exactamente. Se obtendría reducción adicional colocando las estaciones cada 3 millas, a intervalos de 21 millas. Los 30 perfiles requerirían solamente 2700 millas de recorrido, o un tercio del método del cuadrado representado.

En el segundo ejemplo con límites de confidencia de ± 20o/o, se requieren 471 muestras positivas. Nuevamente, asumiendo una proporción de estaciones positivas de 22.62o/o, se podría mejorar esta precisión con 2078 muestras o aproximadamente una muestra por cada 28 millas cuadradas. Disponiendo las muestras cada 3 millas a intervalos de 9 millas, se aproximaría a esta precisión con 71 perfiles de 90 millas de longitud, es decir, con 6400 millas de recorrido.

Para todos los diseños de estudio se tiene que añadir una distancia constante que corresponde a la distancia entre el puerto de embarque y los puntos extremos del área explorada y el recorrido de regreso al puerto. Esto es, aproximadamente, igual al doble de la extensión de la distancia a lo largo de la costa (2 x 640 = 1280 millas, en este ejemplo). La columna 6 da el tiempo necesario para las diferentes actividades del barco: muestreo de huevos, calas y recorrido. La columna 7 contiene el tiempo total del crucero requerido para cada diferente opción de planes de crucero.

También se puede obtener reducción de esfuerzo técnico con el uso de la red CalVET (CalCOFI vertical egg tow net, Red vertical para colección de huevos) que es más pequeña que la red Hensen.

La red CalVET tiene una abertura de 0.05 m^2, alrededor de un octavo del área de la boca de la red Hensen. Será más fácil de manejar desde embarcaciones pequeñas y habrá menor desviación en el muestreo vertical. La muestra a analizar será un octavo de la muestra colectada con red Hensen.

Recomendamos que se inicie el diseño de muestreos semejantes para huevos de sardina, *Sardinops sagax*, y jurel *Trachurus symmetricus murphyi* frente al Perú. Los datos existentes de sardina son suficientes, pero es necesario una mayor información para el jurel.

Las muestras positivas de huevos de la sardina de California son menos numerosas que las de la anchoveta de California. Frente al Perú el número de huevos de sardina por unidad de superficie y la extensión del área de desove se han incrementado desde 1972 (Santander, 1981). En setiembre de 1980, el área de desove de la sardina fue mayor que la del desove de anchoveta y la densidad de huevos de ambas especies fue muy similar.

En el caso del jurel, la abundancia larval es menor que en el caso de la anchoveta y sardina (Santander y S. de Castillo, 1979; S. de Castillo, 1979).

DETERMINATION OF SAMPLING EFFORT REQUIRED FOR ESTIMATING EGG PRODUCTION OF ANCHOVETA, *Engraulis ringens*, OFF PERU

Haydeé Santander[1], Paul E. Smith[2] and Juergen Alheit[3]

1 Instituto del Mar del Perú, Apartado 22, Callao, Perú
2 NOAA, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038, U.S.A.
3 Programa Cooperativo Peruano-Alemán de Investigación Pesquera (PROCOPA).
Instituto del Mar del Perú, Apartado 22, Callao, Perú

ABSTRACT

Existing egg sample data from standard surveys off Peru in the past 20 years have been used for a first aproximation of the number of samples required for a given level of precision of estimate of egg production by the anchoveta per unit of sea surface area. The anchoveta appears to spawn in schools resulting in large proportion of the eggs being taken in a small proportion by the samples. Approximately 8o/o of the positive samples exceeded 4096 eggs per m^2. An important change in the population size of the Peruvian anchoveta has been noted in 1972. The range of egg sample values was similar before and after that change but the mean number of eggs per positive sample was nearly twice as large before the population decline in 1971. Considerations of sample precision and the cost and availability of ship time in the spawning season have been merged to produce a cruise plan with useful projected precision at a reasonable cost. The survey area is 640 miles coastwise and 90 miles offshore and covers 57600 square miles. A 30o/o precision of estimate requires 924 samples and a 20o/o precision requires 2078 samples in this projection. Biases in the estimation of precision are discussed. The log-normal probability distribution is used to describe the positive samples.

INTRODUCTION

The estimation of biomass of fish stocks widely distributed over an oceanic area is notoriously difficult, but often neccesary to enable management of the fishery and prevent inadvertent overfishing. Development of adequate methods for biomass estimates has accompanied the growth of mechanized fishing in the 20th century. Indirect methods include catch analysis and acoustic surveys. Direct methods include quantitative samples of adults and spawning surveys. The spawning survey uses data of fecundity, egg or larval abundance and egg or larval mortality to back-calculate the spawning biomass from the amount of spawn encountered in the water. Problems with existing direct and indirect methods include high costs, low precision caused by low occurrence of the organism and time delay between the estimation of stock size and implementation of fishing controls.

Recently, a direct and instantaneous method which minimizes these disadvantages has been developed (Parker, 1980) and applied (Stauffer and Picquelle, 1980) for estimating the spawning biomass of the northern anchovy, *Engraulis mordax*. Spawning surveys for biomass estimates for multiple spawners, such as the northern anchovy, have to date been hampered by the lack of information on the number of spawnings per year. This problem was solved for the northern anchovy by the studies of Hunter and Goldberg (1979), Hunter and Macewicz (1980) and Hunter and Leong (1981) which revealed that this species spawns about 20 times per year. There is evidence that this also applies to the Peruvian anchovy or anchoveta, *E. ringens* (Santander, Alheit and Smith, manuscript).

The new method is called the "Egg Production Method" (Stauffer and Picquelle, 1980) because the biomass estimate is derived from the estimation of egg production in the spawning area and the egg production rate per unit biomass of the adult portion of the stock.

Egg production in the spawning area is inherently the most variable parameter of this method. The fundamental causes of this are: (1) the eggs are spawned by dense aggregations of adults, (2) the adults spawn for less than half of each day and (3) the eggs are subject to a high mortality rate which may be quite variable. The other parameters are:

- batch fecundity (eggs produced in one night per unit weight of adult female)
- fraction of females spawning each night
- average female weight
- fraction of adult stock weight which is female.

The purpose of this paper is limited to the estimation of egg production in the Peruvian anchoveta spawning area. In the first use of the egg production method (Parker, 1980), the contribution to variance in the estimate of eggs produced per unit area per day was eight times greater than all other parameters combined. Additional sampling in the second application (Stauffer and Picquelle, 1980) reduced the variability to the same level of precision as for the other parameters derived from evaluation of the adult spawning rate. In this paper, the statistical distribution of anchoveta egg samples (Santander and S. de Castillo, 1979) has been used to make a first approximation of the number of eggs samples required to estimate anchoveta egg production rate at several levels of precision. The final objective is to use the convenient sample size in the 1981 estimate of the spawning biomass of the Peruvian anchoveta.

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German fisheries project which is financed by the German Agency for Technical Cooperation (GTZ).

METHODS

To illustrate the methods of statistical analysis for the first estimation of the required number of samples, the results of a 1961 cruise with 59 samples of anchoveta eggs are demonstrated. The geographic and statistical distributions of these samples have been reported by Finarsson, Rojas de Mendiola and Santander (1966).

The first step is to order the egg sample counts from the lowest to the highest number per sample. Since each sample count is 1/59th or the 0.01695th proportion of the sample set, the cumulative frequency is incremented by this fraction for each successively higher sample. The value of each sample is transformed to natural logarithms. This is illustrated in Table 1. In Figure 1 the points in the plot of cumulative sample probability versus the natural logarithm of number of eggs per m^2 is seen to be linear. As a simplifying assumption, the linear (normal probability log-linear) trend for this small sample is assumed to describe the underlying distribution of samples for all anchoveta spawning areas for all time.

To simplify and shorten this somewhat elaborate analysis, one may group the sample values. To illustrate, the sample values of Table 1 and Figure 1 have been grouped in 1-4 eggs per sample, 4-16 eggs per sample, 16-64 eggs per sample, etc. in Table 2. The natural logarithms of the end point of each class are listed as well as the class proportion and cumulative class proportions. In Figure 2, each value is plotted as in Figure 1. Since both lines cross the 50o/o probability line at approximately the same point, the grouping procedure may be seen to be unbiased for this purpose. Also since both lines have approximately the same slope, the grouping procedure is seen to fairly reflect the variance of the original total sample distribution. Since this procedure is satisfactory for this purpose, the subsequent large sample sets gained from Santander and S. de Castillo (1979) are grouped in an identical manner.

Between 1966 and 1979, 911 from a total of 4028 samples from cruises of the IMARPE (mainly Eureka surveys) over the entire spawning area contained anchoveta eggs. The samples were collected during different months. Figure 3 shows the sampling area and the geographic distribution of egg samples before and after 1971. The large sample values from 1966 to 1979 are listed in Table 3. Large values are here considered arbitrarily to be equal or greater than 4096 eggs/m^2. The importance of these large values is that they constitute a large proportion of the eggs in the samples and contribute to the variance. Future surveys must take sufficient numbers of samples to obtain representative amounts of these samples to be precise. The standard error of the mean number of the large samples is 1998 or about 14o/o of the category mean. Smith (1973) concluded that large egg samples are caused by a "mosaic pattern of fish school proportions" and the smaller samples are because "eggs at the perimeter subsequently disperse to a condition of randomness". The range of sample sizes includes one sample of 107376 eggs/m^2, and 78 of the samples exceeded 4096 eggs/m^2. This extreme range of egg population density has also been noted for other schooling fish, e. g. the Pacific sardine, *Sardinops caerulea*, off California (Smith, 1973) and the northern anchovy (Smith, 1981; Smith and Richardson, 1977).

The samples have been taken by the Hensen net which was used vertically from 50 m to the surface (Santander and S. de Castillo, 1979). Two possible sources of underestimation are that, firstly, there may be some anchovy eggs deeper than 50 m and, secondly, the Hensen net may at time filter water more slowly than the net is towed. Two sources of overestimation are that, firstly, the net tow may fish obliquely near the surface and, secondly, the net may filter more water than estimated owing to the reverse cone construction (Tranter and Smith, 1968). For the purpose of this paper, 100o/o filtration and absolutely vertical tows are assumed. The effect of the variability from these sources will be to moderately overestimate the number of samples required for a given precision of egg production. Also samples before and after the change in the Peruvian anchoveta population have been combined since the range of numbers of eggs per sample was similar (Fig. 4). The number of samples with larger numbers of eggs was moderately greater before 1971. Furthermore, the number of samples after 1972 was increased. Samples without anchoveta eggs have been omitted because the size of the spawning area has undergone a massive decrease in 1971, while the geographic coverage of the Eureka surveys has remained approximately the same. The effect of not incorporating the zero samples is to decrease the variance and underestimate the number of samples required for a given precision.

The "Egg Production Method" uses the zero intercept of an exponential mortality curve of aged eggs to estimate egg production. The egg probability distribution data used for estimating sample number from Eureka and other cruises pools anchoveta eggs of all ages. Since anchoveta eggs representing three days spawning may occur in the same sample, this may decrease variance and moderately underestimate the number of samples required. In the proposed 1981 samples the distribution of eggs by age within each sample may be partially independent resulting in an overestimate of the number of samples required.

RESULTS

The frequency distributions of the 911 Peruvian anchoveta egg samples (Table 4) exhibit the same major characteristics as those of the egg samples of the California Pacific sardine and of the northern anchovy (Smith and Richardson, 1977; Table 3.10). Table 4 shows the frequency distributions for the periods before and after 1971. Because of the extreme range of egg densities in the sea, the table is organized in geometric groups with each category encompassing a range of four-fold (i. e. 1-4, 4-16, 16-64, etc.). The representative value of each of the geometrically increasing categories is the geometric mean. For example, the category with 4 to 16 eggs/m^2 is represented by the geometric mean of "8" rather than the arithmetic mean of "10" for the category boundaries (Smith and Richardson, 1977). The largest category is represented by the mean of all values equal to or greater than 4096 eggs/m^2 (see Table 3). As the numbers of samples in the large geometric category are small but important, an unbiased estimate of their category has been used rather than the geometric mean which may be biased.

Table 5 shows the probabilities of the egg sample distribution. Since the population of the Peruvian anchoveta underwent a drastic and relatively long term change in 1971, the distribution of values has been divided at that point. The range of sample values is about the same for both periods, but the mean number of eggs per positive sample declined from an estimated mean value of 2645 eggs/m^2 of sea surface area to a value of 1434 eggs/m^2 - almost a factor of two. The standard deviation of both sets is approximately twice the value of the mean in both cases. The plots of cumulative sample probability versus the natural logarithm of numbers of eggs per m^2 are shown in Figures 5 and 6. Owing to these similarities, for determining a first estimate of the number of samples required for a precise evaluation of anchovy biomass, the two distributions were combined in Table 6. The parameters of the distribution are 2038.5 for the mean and 4425.4 for the standard deviation.

An estimate of the parameters for the population of anchoveta egg densities will in part determine the confidence limits of the number of eggs produced per unit area per night. As a technique for estimating the confidence limits in advance of the survey, the Student t distribution for estimating the confidence limits of the population mean when only a sample mean and a sample standard deviation are known has been applied. The equation is taken from Dixon and Massey (1957, p. 127-128):

$$\bar{X} + \frac{t_{\frac{1}{2}\alpha}\, s}{\sqrt{N}} > \mu > \bar{X} + \frac{t_{1-\frac{1}{2}\alpha}\, s}{\sqrt{N}}$$

Where – μ is the population arithmetic mean
– $\bar{X}$ is the sample arithmetic mean (2038.5)
– t is the confidence limit factor for N-1 degree of freedom and α the probability of being in error (outside the confidence limits)
s is the sample standard deviation (4425.4)
N is the number of samples (911).

These values are fixed for the trial data parameters of mean, standard deviation and number of samples. For planning purposes, the values of α and t should be decided upon and then N may be calculated.

The value of α is the acceptable probability of being in error on the estimate. Frecuently the term "95o/o confidence limits" is used which is equivalent to an α of 0.05. In this case, the calculated confidence limits contain 19 out of 20 estimates. The value of t is a function of the sample size N and the value of α. For $\alpha = 0.05$ and a sample size greater than or equal to 60, t = 2.00. As the number of samples increases, t approaches 1.96. Therefore it is convenient to use t with a value of 2.

The number of samples required may also be determined for any fraction of the mean. For example, should one decide that the sample mean should vary less than 20o/o of the mean below or above the population mean, the number of samples required is given by:

$$N = \left(\frac{t_{\frac{1}{2}\alpha}\, s}{\text{s.e.}} \right)^2$$

Where the notation is as above, except that s.e. stands for the standard error for the mean. The equation can be rewritten

$$N = \left(\frac{t_{1/2\alpha}\, s}{0.2\,\bar{X}} \right)^2$$

Thus with the values t = 2 for all N > 60, s = 4 425.4 (Table 6) for vertical tows of anchoveta eggs and $\bar{X} = 2\,038.5$, the equation is

$$N = \left(\frac{2 \times 4425.4}{0.2 \times 2038.5} \right)^2 = 471$$

When the acceptable error varies from 30o/o to 5o/o of the mean, one gets the following values for the number of positive samples required (positive means samples which contain anchoveta eggs):

(1) For = 0.3 N Pos = 209 N total = 924
(2) For = 0.2 N Pos = 471 N total = 2082
(3) For = 0.1 N Pos = 1885 N total = 8332
(4) For = 0.05 N Pos = 7541 N total = 33331

As the number of positive egg samples, N Pos. is 22.62o/o of the total number of egg samples, N Total, in the data set of Santander and S. de Castillo (1979), assuming that the spawning area is consistent, N Pos. has to be multiplied by 4.42 in order to get the total number of samples, N Total, required.

DISCUSSION

The "Egg Production Method" is a technique for making absolute spawning biomass estimates for the Peruvian anchoveta. Data from the multiple-spawning California northern anchovy may be used with temporal and spatial probability distribution of the Peruvian anchoveta egg samples to establish a first estimate of egg production rate. This egg production rate, integrated over space, may be combined with the egg production per ton of adult fish to produce an instantaneous and absolute estimate of the spawning biomass of the Peruvian anchoveta. The first estimate of biomass and the associated measures of precision will also allow a refinement of the statistical models of precision. The relevant measures of precision will permit the technical effort of estimation of (1) egg production in the spawning area and (2) egg production per unit of biomass to be balanced to achieve the highest technical efficiency. Also, the effort of estimating egg production in the sea can be increased or decreased depending on the specification of the anchoveta management authority and the available funds for conducting the biomass estimate.

One outcome of the egg production method is to subdivide the samples of eggs by stage of development and age since spawning. Preliminary estimates demonstrated that the simultaneous diminution of mean number of eggs per stage and the variation in the number of eggs result in an estimate of required number of samples which is comparable to that of the pooled number of eggs.

The examination of the Hensen net egg data has been used to prepare a first order estimate of the number of samples required to obtain a given precision. The results of this work are demonstrated in Figure 7. It illustrates the fact that increased precision requires many more samples. Provided the samples are independent, the precision improves by a factor of two with each increase in the sampling effort by a factor of four.

The cruise plan for an egg production estimate of the spawing biomass of *E. ringens* depends on several factors, including the precision required, the proportion of the survey area covered by anchoveta spawning and the relative number of transects and stations per transect. For the purpose of planning, three sampling precision levels have been erected (Table 7, column 1), based on the results of the Hensen net samples (Table 4, 5, 6). The planned survey area stretches 640 nautical miles along the Peruvian coastline and 90 miles offshore, and thus covers 57600 nautical square miles. If, for example, the precision chosen is ± 30o/o (Table 7, column 1), then 209 positive samples are required (column 2). Also, if as in the Hensen samples set used here, the proportion of positive stations is 22.62o/o, the total number of samples required is 924 (column 2). With a total survey area of 57600 mi^2, this would require that about 64 mi^2 be represented by each sample. This could be accomplished by subdividing the survey area into squares, in this case into 8 x 8 mi squares (column 3). There is some merit in each sample representing a square unit of area. However, as the square unit requires the maximum ship travel and time of survey, other options are explored. Frequently, coastal transects are spaced further apart to reduce ship travel time. If the stations were spaced 4 mi apart, the transect lines could be spaced 16 mi apart (column 3) to maintain equal density. The number of transects in the 640 mi coastal section would be reduced from 80 to 40 (column 4). This would result in a saving of ship travel cost along the transects from 7200 mi to 3600 mi (column 5), a reduction of exactly 50o/o. Further reduction could be accomplished by having the stations 3 mi apart at 21 mi intervals. The 30 transects of stations would require only 2700 mi of line travel, or one third of the represented square method.

In the second example with ± 20o/o confidence limits, 471 positive samples are required. Again, assuming 22.62o/o positive, one could achieve this precision with 2078 samples or about one sample for each 28 square miles. Samples 3 mi apart at 9 mi intervals would approach this precision with 71 transect of 90 mi length, i.e. 6400 survey track miles.

For all miles traveled, one has to add a constant for all survey designs which corresponds to the distance traveled from the embarcation port to the outer ranges of the survey area and back to the port. This is approximately equal to two times the survey extent along the coast (2 x 640 = 1280 mi in this example). Column 6 gives the time needed for the different ship activities: egg tow samples, trawls and travel. Column 7 lists the total cruise time required for each of the different options of cruise plans.

Reduction of technical effort can also be achieved by the use of the newly designed CaVET-Net (calCOFI vertical egg tow net) which is smaller than the Hensen egg net. It has an opening of 0,05 m^2, about an eighth of the Hensen egg net mouth area. The net will be easier to manipulate from small ships and will stray less from the vertical. Also, the sample to be sorted will be an eighth of that of the Hensen net.

We recommend that similar sampling design studies begin for the eggs of sardine, *Sardinops sagax*, and jack mackerel, *Trachurus symmetricus murphyi*, off Peru. Existing data will suffice for the sardine but more information will be necessary for the jack mackerel.

The sardine of California is somewhat less numerous in positive samples than the Californian anchovy. Off Peru the numbers of egg of sardines per unit surface area and the spawning area are increasing since 1972 (Santander, 1981). In September 1980, the spawning area of the sardine was larger than that of the anchovy and the egg densities of both species were very similar.

In the case of the jack mackerel, the larval abundance is less numerous than that of anchoveta and sardine (Santander and S. de Castillo, 1979; S. de Castillo, 1979).

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Tabla 1 Distribución de frecuencias y probabilidades de las muestras de huevos de anchoveta sin agrupar en agosto de 1961 (según Einarsson , Rojas de Mendiola y Santander, 1966 - modificado.).

Table 1 Frequency distribution (ungrouped) and probability of anchoveta egg samples from August 1961 (modified after Einarsson, Rojas de Mendiola and Santander, 1966).

NUMERO DE HUEVOS/m² NUMBER EGGS/m² (x)	ln (x) ln (x)	FRECUENCIA SAMPLE FREQUENCY	PROBABILIDAD DE LA MUESTRA SAMPLE PROBABILITY	PROBABILIDAD ACUMULADA DE LA MUESTRA CUMULATIVE SAMPLE PROBABILITY
3	1.10	6	0.1017	0.1017
6	1.79	3	0.0508	0.1525
9	2.20	2	0.0339	0.1864
12	2.48	3	0.0508	0.2373
15	2.71	2	0.0339	0.2712
18	2.89	1	0.0169	0.2881
21	3.04	3	0.0508	0.3390
24	3.18	1	0.0169	0.3559
27	3.30	1	0.0169	0.3729
30	3.40	1	0.0169	0.3898
36	3.58	1	0.0169	0.4068
45	3.81	1	0.0169	0.4237
51	3.93	1	0.0169	0.4407
57	4.04	1	0.0169	0.4576
72	4.28	1	0.0169	0.4746
78	4.36	1	0.0169	0.4925
84	4.43	1	0.0169	0.5085
87	4.47	1	0.0169	0.5354
99	4.60	1	0.0169	0.5424
108	4.68	1	0.0169	0.5593
120	4.79	1	0.0169	0.5763
126	4.84	1	0.0169	0.5932
153	5.03	1	0.0169	0.6102
183	5.21	1	0.0169	0.6271
309	5.73	1	0.0169	0.6441
312	5.74	1	0.0169	0.6610
324	5.78	1	0.0169	0.6780
357	5.88	1	0.0169	0.6949
393	5.97	1	0.0169	0.7119
459	6.13	1	0.0169	0.7288
474	6.16	1	0.0169	0.7458
492	6.20	1	0.0169	0.7627
612	6.42	1	0.0169	0.7797
630	6.45	1	0.0169	0.7966
804	6.69	1	0.0169	0.8136
858	6.75	1	0.0169	0.8305
1041	6.95	1	0.0169	0.8475
1128	7.03	1	0.0169	0.8644
1470	7.29	1	0.0169	0.8814
1677	7.42	1	0.0169	0.8983
1992	7.60	1	0.0169	0.9153
2637	7.88	1	0.0169	0.9322
4557	8.42	1	0.0169	0.9492
4710	8.46	1	0.0169	0.9661
4887	8.49	1	0.0169	0.9831
5703	8.65	1	0.0169	1.0000

NUMERO DE HUEVOS/m² NUMBER EGGS/m² (x)	ln (x) ln (x)	FRECUENCIA SAMPLE FREQUENCY	PROBABILIDAD SAMPLE PROBABILITY	PROBABILIDAD ACUMULADA DE LA MUESTRA CUMULATIVE SAMPLE PROBABILITY
1 - 4	1.39	6	0.1017	0.1017
4 - 16	2.77	10	0.1695	0.2712
16 - 64	4.16	11	0.1864	0.4576
64 - 256	5.55	10	0.1695	0.6271
256 - 1024	6.93	12	0.2034	0.8305
1024 - 4096	8.32	6	0.1017	0.9322
4096 +		4	0.0678	1.0000

Tabla 2 Distribución de frecuencias y probabilidades agrupadas de las muestras de huevos de anchoveta en agosto de 1961 (según Einarsson, Rojas de Mendiola y Santander, 1966 - modificado)

Table 2 Frequency distribution (grouped) and probability of anchoveta egg samples from August 1961 (modified after Einarsson, Rojas de Mendiola and Santander, 1966).

4 128	5 688	11 355
4 140	5 820	13 362
4 140	6 264	13 788
4 164	6 336	13 824
4 368	6 516	14 400
4 396	7 008	15 120
4 401	7 110	15 120
4 545	7 152	15 936
4 635	7 515	16 107
4 650	7 728	16 140
4 656	7 980	18 576
4 656	8 010	21 096
4 680	8 535	22 344
4 716	8 640	22 560
4 758	8 868	22 956
4 845	9 072	23 004
4 845	9 132	24 060
4 848	9 204	24 288
4 944	9 300	25 872
5 040	9 360	27 192
5 088	9 984	29 565
5 172	10 200	42 792
5 268	10 344	57 400
5 322	10 524	74 496
5 424	10 728	81 876
5 652	10 884	107 376

Tabla 3 Muestras con gran número de huevos de anchoveta, 1966-1979.

Table 3 Samples with large anchoveta egg numbers from 1966-1979.

NUMERO DE HUEVOS/m² NUMBER EGGS/m²	1-4	4-16	16-64	64-256	256-1024	1024-4096	4096+	TOTAL
PROMEDIO GEOMETRICO GEOMETRIC MEAN	2	8	32	128	512	2048	14256	
CRUCERO CRUISE								
6602	4	3	6	3	0	0	0	16
6608	1	1	1	0	0	0	0	3
6609	0	3	5	9	13	11	18	59
6611	2	1	5	4	6	3	2	23
6702	1	4	4	1	2	2	1	15
6705	1	1	1	0	1	0	0	4
6709	6	4	11	14	9	13	9	66
6711	3	1	4	3	4	4	2	21
7207	7	9	4	5	4	8	2	39
7208	13	3	4	20	9	7	1	57
7209	13	7	10	8	19	7	7	71
7210	0	1	6	11	4	8	0	30
7301	0	4	8	7	2	10	3	34
7309	12	18	15	23	15	8	4	95
7311	7	12	11	12	14	12	7	75
7807	10	22	25	18	25	16	10	126
7902	18	12	11	10	3	6	3	63
7909	17	19	15	12	20	17	14	114
AÑOS YEARS								
1966-1967	18	18	37	34	35	33	32	
1972-1979	97	107	109	126	115	99	51	911

Tabla 4 Distribución de frecuencias agrupadas de muestras de huevos de anchoveta de 1966 a 1979.

Table 4 Group frequency distributions of anchoveta egg samples from 1966-1979.

NUMERO DE HUEVOS/m^2 NUMBER EGGS/m^2 (x)	ln (x) ln (x)	FRECUENCIA FREQUENCY	PROBABILIDAD SAMPLE PROBABILITY	PROBABILIDAD ACUMULADA DE LA MUESTRA CUMULATIVE SAMPLE PROBABILITY
1966 - 1967				
1 - 4	1.39	18	0.0870	0.0870
4 - 16	2.77	18	0.0870	0.1739
16 - 64	4.16	37	0.1787	0.3527
64 - 256	5.55	34	0.1643	0.5169
256 - 1024	6.93	35	0.1691	0.6860
1024 - 4096	8.32	33	0.1594	0.8454
4096 +		32	0.1546	1.0000
1972 - 1979				
1 - 4	1.39	97	0.1378	0.1378
4 - 16	2.77	107	0.1520	0.2898
16 - 64	4.16	109	0.1548	0.4446
64 - 256	5.55	126	0.1790	0.6236
256 - 1024	6.93	115	0.1634	0.7869
1024 - 4096	8.32	99	0.1406	0.9276
4096 +		51	0.0724	1.0000

Tabla 5 Distribución de frecuencias y probabilidades agrupadas de muestras de huevos de anchoveta de 1966 a 1979.

Table 5 Group frequency distribution and probability of anchoveta egg samples from 1966-1979.

NUMERO DE HUEVOS/m^2 NUMBER EGGS/m^2	1966 - 1967		1972 - 1979		1966 - 1979
	FRECUENCIA FREQUENCY	PROBABILIDAD PROBABILITY	FRECUENCIA FREQUENCY	PROBABILIDAD PROBABILITY	PROBABILIDAD PROMEDIO MEAN PROBABILITY
1 - 4	18	0.0870	97	0.1378	0.1124
4 - 16	18	0.0870	107	0.1520	0.1195
16 - 64	37	0.1787	109	0.1548	0.1668
64 - 256	34	0.1643	126	0.1790	0.1717
256 - 1024	35	0.1691	115	0.1634	0.1663
1024 - 4096	33	0.1594	99	0.1406	0.1500
4096 +	32	0.1546	51	0.0724	0.1135
NUMERO PROMEDIO DE HUEVOS/MUESTRA MEAN NUMBER EGGS/SAMPLE	2644.5		1433.7		2038.5
S.D.	5026.2		3649.9		4425.4

Tabla 6 Probabilidad promedio y número promedio de huevos de anchoveta por muestra de 1966 a 1979.

Table 6 Mean probability and mean number of eggs per sample of anchoveta egg samples from 1966-1979.

NIVEL DE PRECISION PRECISION LEVEL	NUMERO DE MUESTRAS DE HUEVOS NUMBER OF EGGS SAMPLES		CONFORMACION DE LA UNIDAD DE MUESTRA SELECCIONADA SELECTED SHAPE OF SAMPLE UNIT (MILES)	NUMERO DE TRANSECTOS NUMBER OF TRANSECTS	DISTANCIA TOTAL + 1280 mi TOTAL DISTANCE (+1280 mi)	TIEMPO (DIAS) TIME (DAYS)			DURACION DEL CRUCERO (DIAS) CRUISE TIME (DAYS)
	POSITIVAS POSITIVE	TOTAL				MUESTRAS DE HUEVOS EGG SAMPLES	ARRASTRE TRAWLS	NAVEGACION TRAVEL	
± 30 %	209	924	8 x 8	80	7200	10	5	29	44
			4 x 16	40	3600	10	5	17	32
			3 x 21	30	2700	10	5	14	29
± 20 %	471	2082	5.3 x 5.3	121	10980	22	5	43	70
			4 x 7	91	8200	22	5	33	60
			3 x 9	71	6400	22	5	27	54
± 10 %	1885	8332	2.6 x 2.6	246	22140	87	5	81	173

Tabla 7 Tabla para decisión de diseños de exploración
Table 7 Decision chart for survey design.

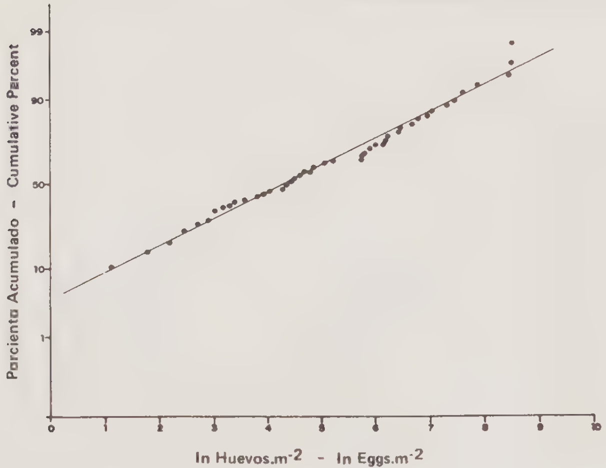

Figura 1

Ploteo de la distribución porcentual acumulada sin agrupar vs. el 1n del número de huevos por m^2 en papel de probabilidad normal. Muestras de huevos de anchoveta de agosto 1961 (según Einarsson, Rojas de Mendiola y Santander, 1966 – Modificado).

Figure 1

Plot of ungrouped cumulative percent distribution vs 1n Nr of eggs per m^2 on normal probability paper. Anchoveta egg samples from August 1961 (modified after Einarsson, Rojas de Mendiola and Santander, 1966).

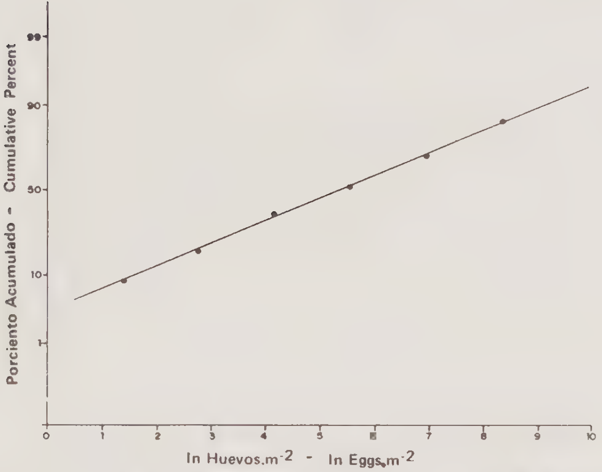

Figura 2

Ploteo de la distribución porcentual acumulada agrupada vs. el 1n del número de huevos por m^2 en papel de probabilidad normal. Muestras de huevos de anchoveta de agosto 1961 (según Einarsson, Rojas de Mendiola y Santander, 1966 - Modificado)

Figure 2

Plot of grouped cumulative percent distribution vs. 1n Nr. of eggs per m^2 on normal probability paper. Anchoveta egg samples from August 1961 (modified after Einarsson, Rojas de Mendiola and Santander, 1966).

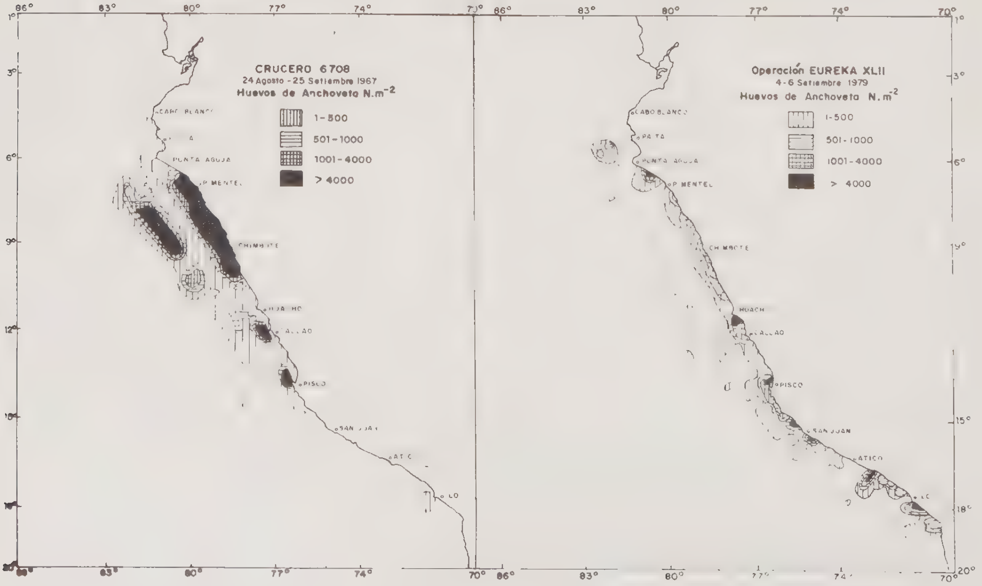
CRUCERO 6708
24 Agosto - 25 Setiembre 1967
Huevos de Anchoveta N.m-2
1-500
501-1000
1001-4000
> 4000
PUNTA AGUJA
P MENTEL
CHIMBOTE
CALLAO
PISCO
SAN JUAN
Operación EUREKA XLII
4-6 Setiembre 1979
Huevos de Anchoveta N.m-2
1-500
501-1000
1001-4000
> 4000
CABO BLANCO
PAITA
PUNTA AGUJA
P MENTEL
CHIMBOTE
HUACH
CALLAO
PISCO
SAN JUAN
ATICO
86°
83°
80°
77°
74°
70°
1°
3°
6°
9°
12°
15°
18°
20°

Figura 3 Area de muestreo y distribución geográfica de muestras de huevos de anchoveta antes y después de 1971.

Figure 3 Sampling area and geographic distribution of anchoveta egg samples before and after 1971.

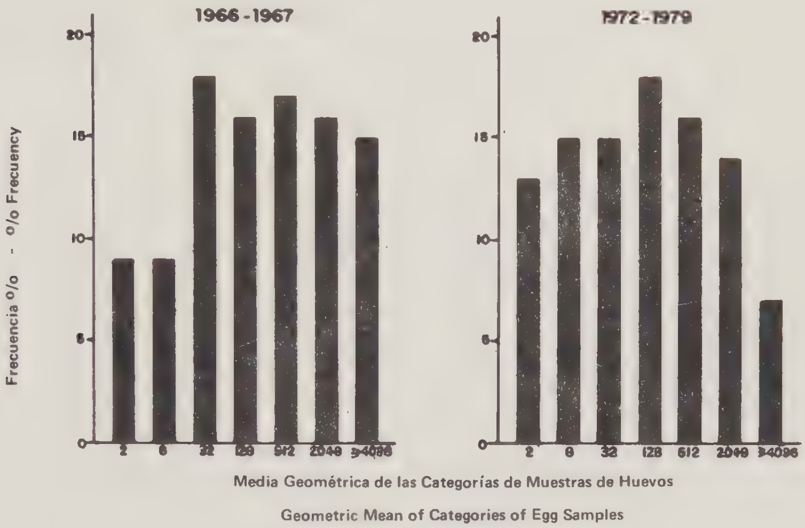

Figura 4 Comparación de la distribución de frecuencias, en por ciento, de las muestras de huevos antes y después de 1971.

Figure 4 Comparison of percent egg sample frecuency distribution before and after 1971.

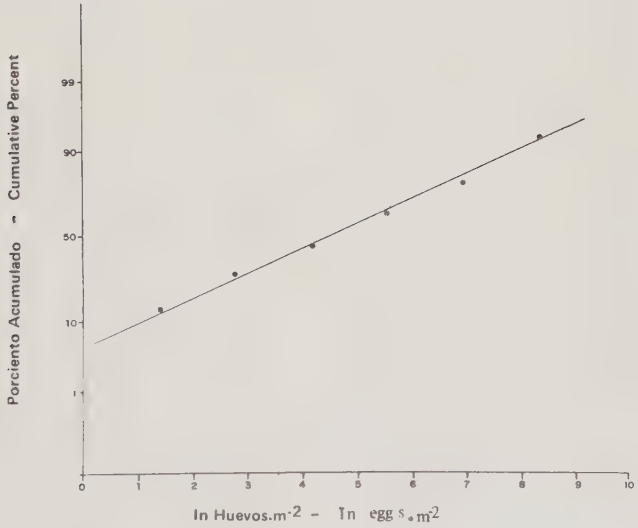

Figura 5 Ploteo de la distribución porcentual acumulada, agrupada y en por ciento, versus número de huevos por m^2 en papel de probabilidad normal. Muestras de huevos de anchoveta de 1966-1967.

Figure 5 Plot of grouped cumulative percent distribution versus ln of the Nr. of eggs per m^2 on normal probability paper. Anchoveta egg samples from 1966-1967.

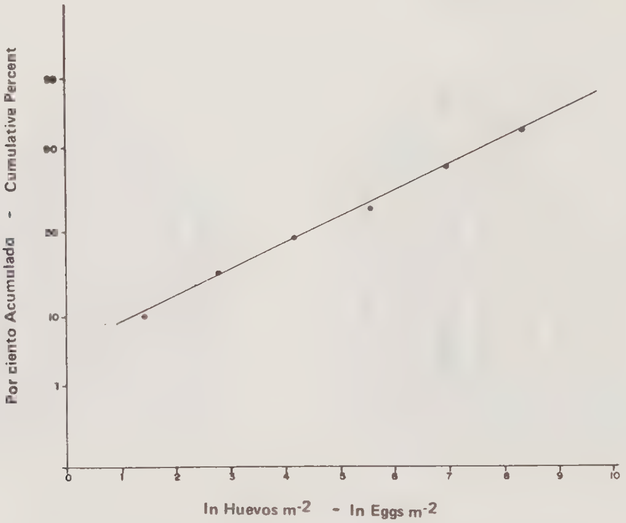

Figura 6 Ploteo de la distribución porcentual acumulada, agrupada y en por ciento, versus número de huevos por m^2 en papel de probabilidad normal. Muestras de huevos de anchoveta de 1972 a 1979.

Figure 6 Plot of grouped cumulative percent distribution versus ln Nr. of eggs per m^2 on normal probability paper. Anchoveta egg samples from 1972-1979.

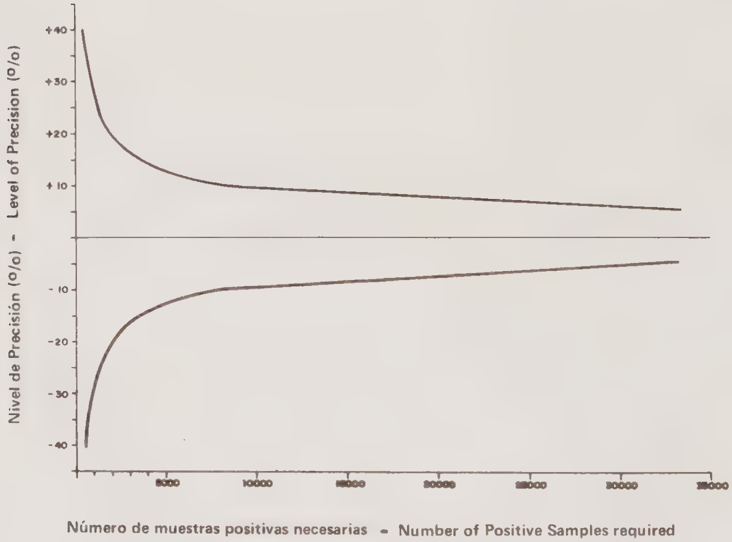

Figura 7 Relación entre la precisión y el número de muestras requerido en el muestreo de huevos de la anchoveta peruana.

Figure 7 Relationship between precision and number of samples required for egg samples of Peruvian anchoveta.

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AN *IN SITU* DEVICE FOR SENSING AND COLLECTING MICROPLANKTON

EDWARD D. SCURA[1]
National Oceanic and Atmospheric Administration
National Marine Fisheries Sevice
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

This report describes a simple system that was developed to search for and collect ''patches'' of microzooplankton at sea. It consists of a shipboard diaphragm pump, 50 meters of vacuum hose, and an *in situ* particle sensor attached to the influent end of the hose. This system was used to collect water at discrete depths while the particle concentration of the water was continuously monitored as it entered the pump hose.

Laboratory tests showed no significant avoidance by live microzooplankton of the particle sensor or the collecting device. There appeared to be no difference in the mortalities of organisms that were pumped through the system compared with those that did not pass through the system. In addition, laboratory tests indicate that small, high-density patches of microzooplankton can be collected with minimal smearing of the sample.

The device was tested in several sea trials off the southern California coast, in the New York Bight, and in the Austnesfjorden near Lofoten, Norway. In Austnesfjorden, a water sample was collected that contained 0.6 micronauplii/ml. This is believed to be the highest concentration of micronauplii ever collected.

RESUMEN

En este trabajo se describe un mecanismo sencillo, ideado para encontrar y recolectar en el mar, concentraciones de micro-zooplancton. Se utiliza a bordo una bomba de diafragma con 50 metros de tubo de vacío y un sensor de partículas *in situ* adaptado a la extremidad del tubo. Este sistema fué usado para recoger agua a ciertas profundidades, controlando continuamente las partículas que entraban con el agua.

Los análisis en el laboratorio no indicaron que los integrantes vivos del micro-zooplancton escapasen al sensor de partículas o al dispositivo de recolección. No se observó diferencia en la mortalidad de organismos obtenidos mediante este sistema y los que no sufrieron la acción del mismo. Los análisis de laboratorio indican además, que los organismos experimentan una fricción mínima al ser obtenidos de pequeñas zonas en el mar donde aparecían con densidad de población elevada.

El dispositivo mencionado se probó repetidas veces en el mar, cerca de la costa sur de California, en la bahía de Nueva York y en Austnesfjorden cerca de Lofoten (Noruega). En Austnesfjorden se tomaron muestras de agua que contenian 0.6 micro-nauplios por ml., y se se considera que esta concentración es la máxima obtenida hasta la fecha.

INTRODUCTION

Although it is widely recognized that the distribution of marine plankton is not random (Boyd 1973), little is known about the microstructure of the upper mixed layer because of the limitations of conventional collecting devices. Plankton nets sample large volumes of water and therefore lack the resolution necessary to detect the small-scale structure of planktonic communities. Fisheries biologists, in particular, need to study the microdistribution of marine plankton because of an apparent contradiction in many investigations of larval fish survival at sea. Several laboratory studies with pelagic fish larvae indicate that the concentration of appropriate food organisms required for moderate growth and survival is generally higher than the density of analogous organisms found in the spawning grounds (May 1974). Most observers agree that this discrepancy results from the inadequacies of conventional plankton-sampling schemes; that is, although plankton nets give mean densities of plankton in a scale of thousands of cubic meters, this information can be misleading because microzooplankton densities can vary by more than 2 or 3 times in a scale of less than a meter (Owen 1981). Since the searching volume of a fish larva is generally less than 100 liters per day (Blaxter 1966; Rosenthal and Hempel 1970; Hunter 1972) it is obvious that a description of plankton distribution on the meter scale or less is necessary to understand the feeding dynamics of fish larvae.

Recently developed *in situ* particle counters can detect the number and sizes of individual plankters with spatial resolution in the scale of centimeters (Boyd and Johnson 1969; Maddux and Kanwisher 1965). Although these instruments are useful for studying the microstructure of planktonic com-

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[1] Present Address:
Aquatic Farms Ltd.
49-139 Kamehameha Highway
Kaneohe, Hawaii 96744

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munities, they do not collect discrete samples of monitored water. I found this to be a serious limitation for my work on larval fish survival at sea. Fish larvae are selective predators, and feeding success depends on a number of factors including the type, density, and size of the prey (Lasker 1975; Scura and Jerde 1977). Also the food selected by fish larvae can differ in nutritional value (Lasker et al. 1970; Scura and Jerde 1977). To study these relationships and their effect on larval survival one must collect discrete samples of seawater from various locations within the spawning grounds so that the densities, size frequency distributions, and species of the prey can be determined.

If seawater samples can be collected without injuring the prey or altering their concentration, then feeding experiments can be conducted by introducing laboratory-produced fish larvae into the seawater samples. This technique can be used to determine feeding thresholds and prey preferences of fish larvae at various developmental stages.

Lasker (1975) established feeding criteria for first-feeding anchovy larvae *(Engraulis mordax)* in waters collected from the chlorophyll maximum layers off the southern California coast. He used an *in situ* pump in conjunction with a shipboard fluorometer to find aggregations of the naked dinoflagellate *Gymnodinium splendens* that were rich enough to initiate feeding in early post-yolk-sac anchovy larvae. Although *G. splendens* is a good food for first-feeding anchovy larvae, older larvae require larger particles (e.g., copepod nauplii) to meet their energy needs (Hunter 1972). Lasker was unable to find aggregations of microzooplankton rich enough to support substantial feeding by anchovy larvae because his fluorometric technique was only useful for detecting phytoplankton. Although zooplankton may aggregate in or near chlorophyll maxima (Mullin and Brooks 1972), Lasker had no way of monitoring zooplankton concentrations other than by random discrete sampling, which was found to be ineffective.

In this report I describe a simple system to search for and collect ''patches'' of microzooplankton. It consists of a shipboard diaphragm pump that samples water from discrete depths and a particle sensor that continuously monitors the particle concentration of the water as it enters the pump hose.

This system has been used in several sea trials off the southern California coast, in the New York Bight, and in the Austnesfjorden in the Lofoten area of Norway.

DESCRIPTION OF THE DEVICE

The system for sensing and collecting microplankton is made up of two components: (1) a shipboard diaphragm pump (Jabsco Model #34600) capable of pumping 25 to 30 liters of water per minute through 50 meters of 2.5-cm. I.D. vacuum hose (Gemline light duty) and (2) a particle-detecting system that consists of an *in situ* continuous-flow particle sensor that independently samples water from a point adjacent to the influent end of the pump hose. The particle sensor is connected to a shipboard Coulter Counter Model A by a shielded cable, which is taped along the length of the pump hose. The Model A was modified by connecting an integrator buffer gain control as illustrated in the circuit diagram in Figure 1. The output from the integrator connects to a multiple-voltage range recorder. The impulses from the particle sensor are integrated so that increases in counting rate (i.e., higher particle concentration) deflect the recorder pen from the baseline. The response is proportional to the counting rate, so knowledge of the flow rate through the particle sensor can be used to calibrate the instrument to give the concentration of particles in the water. However, I did not rely on the instrument for precise particle counts because of the possibility of erroneous counts due to electrical interference, air bubbles, or nonliving particles. This instrument was designed as a searching and collecting device. If the detector response indicated a region with high particle concentration, it was easy to collect the water from the pump effluent for detailed shipboard examination with either a microscope or a Coulter Counter Model T_A, or for preservation for later laboratory analysis.

The particle sensor operates on the Coulter Counter principle. Seawater passes through a 3-mm tube containing two electrodes separated by a 1-mm aperture (Figure 2). The seawater acts as the electrolyte, and a current is induced between the electrodes. As a particle passes through the aperture, the resistance between the electrodes is changed proportionally to the volume and impedance of the particle.

The particle sensor was machined from a 1.9-cm-diameter solid Lexan rod (Figure 2). The electrodes consisted of 2-cm squares of platinum foil that were welded to the leads from the shielded cable. Prior to welding, the leads were passed through the electrode component and out the particle sensor end of the 3-mm passage by way of a small hole drilled in the side of the electrode component (Figure 2). After welding, the foil was rolled into a cylinder and fitted into the 3-mm passage of the electrode component by pulling back on the lead from the shielded cable. The length of exposed lead from the shielded cable to the electrode component was then imbedded in a flexible urethane resin to insulate against electrical leakage. The electrode components were removable so that the sensor could be disassembled in case the aperture became

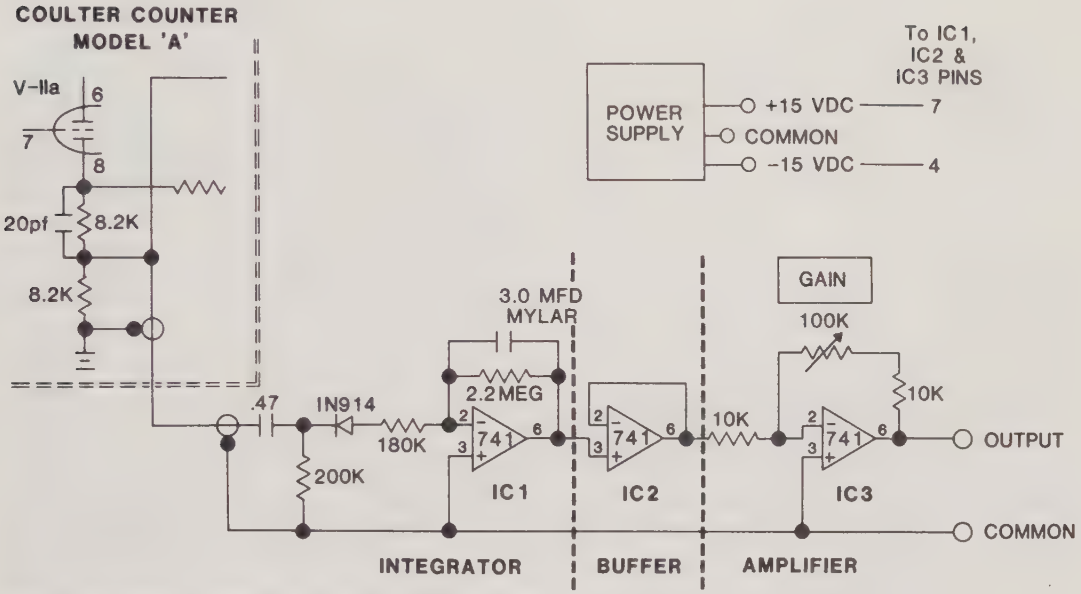
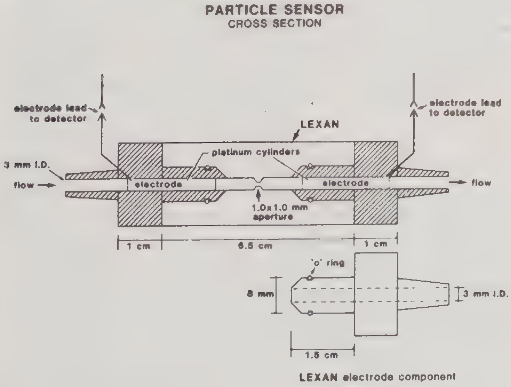

COULTER COUNTER
MODEL 'A'
V-IIa
6
7
8
20pf
8.2K
8.2K
To IC1,
IC2 &
IC3 PINS
POWER
SUPPLY
+15 VDC
7
COMMON
-15 VDC
4
3.0 MFD
MYLAR
2.2MEG
.47
IN914
180K
200K
2
3
741
6
IC1
IC2
IC3
GAIN
100K
10K
10K
OUTPUT
COMMON
INTEGRATOR
BUFFER
AMPLIFIER

Figure 1. Circuit diagram for modified Coulter Counter Model A particle counter.

clogged (something that has not happened during 45 days of sea trial).

Water is pumped through the sensor at a rate of 200 ± 10 ml/minute by a vacuum created from connecting the effluent end of the particle sensor to the intake of the pump hose as illustrated in Figure 3. This connection was made with a 2-M-by-3-mm I.D. tygon tube to insure that the electrical resistance through the aperture between the electrodes is much less than by any other route. For the same reason, the intake for the particle detector was connected to a 30-cm-by-3-mm I.D. tygon tube. The connections between electrodes and the shielded cable (that transmitted the signal to the ship) were imbedded in a flexible urethane resin to insulate against electrical leakage.


PARTICLE SENSOR
CROSS SECTION
electrode lead
to detector
electrode lead
to detector
LEXAN
platinum cylinders
3 mm I.D.
flow
electrode
electrode
flow
1.0x1.0 mm
aperture
1 cm
6.5 cm
1 cm
'o' ring
8 mm
3 mm I.D.
1.5 cm
LEXAN electrode component

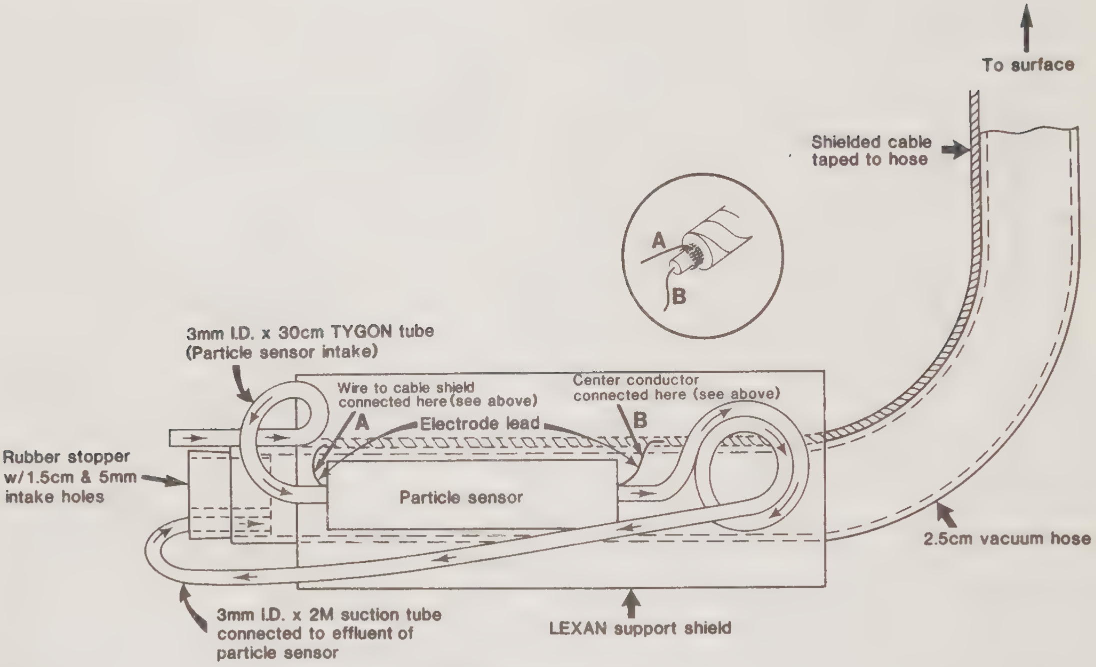
30 cm x 3 mm I.D. tube connected to inlet
2 M x 3mm I.D. tube connected to effluent

Figure 2. Particle sensor.

OPERATION

To operate the system, the sample probe, which consists of the influent end of the pump hose with attached particle sensor, is attached to a weighted (20 kilos) hydrowire and slowly lowered through the water column with the pump and the particle detector in operation. Depths are taken from the winch-metering device and called out to the operator, who records them on the chart paper adjacent to the corresponding response on the recorder. Using this technique, it is possible to get a vertical profile of the particle distribution to a depth of 35 m. Longer lengths of hose could be used to study the particle distribution to greater depths, but it was not needed for our work.

The detector responds to the particle concentration in the water within 2 seconds after the water enters the pump hose; it takes 60 seconds for the water to pass through the hose to the deck of the ship. It is therefore a simple matter for the operator to collect a discrete water sample at the effluent end of the pump system 58 seconds after observing an interesting response on the recorder. Occasionally particle sizes overlap,


To surface
Shielded cable taped to hose
A
B
3mm I.D. x 30cm TYGON tube (Particle sensor intake)
Wire to cable shield connected here (see above)
A
Electrode lead
Center conductor connected here (see above)
B
Rubber stopper w/1.5cm & 5mm intake holes
Particle sensor
2.5cm vacuum hose
3mm I.D. x 2M suction tube connected to effluent of particle sensor
LEXAN support shield

SAMPLE PROBE

Figure 3.

making it difficult to detect the smaller micronauplii. Such is the case when the concentration of larger phytoplankton (e.g., *Ceratium sp.*) is sufficiently high to mask the presence of the less-concentrated microzooplankton. Careful manipulation of the instrument's threshold adjustment is important at such times.

The particle sensor operates on direct current so that the polarity of the electrodes must be reversed approximately every minute to prevent a change in sensitivity due to plating of the electrodes. This is easily accomplished on the Coulter Counter Model A by tripping the reset switch.

PERFORMANCE

With any plankton-collecting device, there is always the question of avoidance. This system has two separate components that sample plankton. One is the diaphragm pump, which samples at a rate of 25 to 30 l/min through a 1.5-cm orifice; the other is the particle sensor, which samples at a rate of 90 to 210 ml/min through a 3-mm orifice. Although larger zooplankters are likely to avoid such slow influent currents, this system was designed to collect microzooplankton smaller than 600 μm. To test for this, wild plankton were collected off La Jolla, California, in a 42-μm plankton net.

Back in the laboratory, the plankton were filtered through a 560-μm screen and collected on a 64-μm screen. The plankton were allowed to settle for 2 hours to eliminate those killed by handling. Then they were added to a tank containing 400 liters of filtered seawater to make a final concentration of 0.8 ± 0.3 organisms/ml (± 2 S.D.). This concentration was chosen because it is within the range that might be expected in a plankton patch at sea. The particle-pumping system was started in a separate tank containing filtered seawater, and once normal pumping was established, the sample probe was transferred into the tank containing the microplankton. Pumping was resumed for 2 minutes, and after 70 seconds, six 1-liter samples were collected and the plankton concentration determined. If plankton in the 64 to 560-μm size range are capable of avoiding the influent current of the particle-pumping system, then the concentration of particles in the pumped water should have been less than in the tank. The mean ± 2 S.D. for the pumped samples was 0.7 ± 0.3 organisms/ml, which was not significantly different from the water in the tank (0.8 organisms/ml).

To test for microzooplankton's avoidance of the particle sensor, a 3-mm I.D. tube was connected to a peristaltic pump set at a flow rate of 200 ml/min. The influent end of the tube was placed in a 4-liter beaker filled with seawater containing microzooplankton (64-560 μm) at a concentration of 1.5 ± 0.4 organisms/ml (± 2 S.D.). Four 10-ml samples were collected over a 2-minute period, and the particle concentration was determined. The mean ± 2 S.D. for the pumped water was 1.7 ± 0.6 organisms/ml. This test was repeated with seawater containing 0.5 ± 0.2 organisms/ml, and the pumped water contained 0.5 ± 0.1 organisms/ml.

INJURY

If this system is to be used to collect seawater for feeding experiments with fish larvae, it is important that the prey organisms not be injured. A diaphragm pump was selected for this system in the belief that it would be less harmful to plankton than a centrifugal pump. To test for injury to microzooplankton during collection, seawater containing 0.8 organisms/ml (the same organisms that were collected for the avoidance experiments) was pumped through the system and collected in two 2-liter separatory funnels. Identical but unpumped seawater was also collected in two 2-liter separatory funnels. The 4 funnels were left undisturbed for 4 hours in a temperature-controlled room at 17 ± 1°C. Then 25 ml of the seawater were drawn from the bottom and the number of organisms counted. After 24 hours, another 25 ml were collected and counted from the same funnels. There appeared to be no difference in the mortalities of organisms that were pumped through the system compared to those that did not pass through the system (Table 1). The high number of mortalities during the first 4 hours was probably due to injuries resulting from the excessive handling required to capture the zooplankton and separate out the 64-to-560-μm size range.

SMEARING

If the distribution of plankton is highly contagious in a region, then the sample probe might quickly pass from high-particle-density seawater to lower density. Depending on the flow characteristics through the hose and pump, the sampled water can smear during the collecting process so that it is difficult to collect seawater with representative plankton concentrations.

To test for smearing, normal pumping was established with the sample probe immersed in a tank of filtered seawater. A 1-liter "square wave" of high-particle-density seawater was introduced into the pumping system with an underwater connection between the sample probe and a 1.5-cm I.D. tube connected to a graduated cylinder containing seawater with 135 rotifers/ml *(Brachionus plicatilis)*. No air bubbles were introduced into the pumping system using this technique. (Air bubbles would disrupt the flow characteristics in the pump and hose.) Normal pumping of the filtered seawater was resumed after the 1 liter of seawater containing the rotifers was introduced. Fifteen 1-liter samples were collected in sequence from the pump effluent starting at 40 seconds after the rotifers were sampled, and the concentration of rotifers in each 1-liter sample was determined. There was minimal smearing: 94 percent of the rotifers introduced in 1 liter were recovered in 3 liters of discharge water.

TABLE 1

Comparison of Microplankton Mortality in Water Passed and Not Passed through a Diaphragm Pump

	Pump Number of organisms/25 ml		*No pump* Number of organisms/25 ml	
	Funnel #1	Funnel #2	Funnel #1	Funnel #2
4 hours	344	295	300	252
24 hours	27	41	35	43

FIELD TRIALS

The device for sensing and collecting microplankton was tested in several sea trials off the southern California coast, in the New York Bight, and in the Austnesfjorden in the Lofoten area of Norway. The system was tested by comparing the particle concentration in discrete samples of seawater collected from the pump to the corresponding response of the detector. A good correlation was found between the response of the detecting system and the actual concentration of particles in the sampled water as determined by direct microscopic counts.

Figure 4 depicts the chart recordings of the vertical distribution of particles at one station in Austnesfjorden, Norway, on two separate days. Discrete samples were collected from the pump at various depths, and the concentrations of nauplii were determined by microscopic counts. At 2230 hours on May 15, 1977, we found a concentration of 0.6 nauplii/ml near the surface. The mean carapace length of the nauplii was 250 μm S.D. ± 48 μm (n = 50). To our knowledge, this is the highest concentration of micronauplii ever collected at sea. It is interesting to note the contagious nature of the particle distribution. For instance, within 3 meters of the surface, the nauplii concentration had dropped by a factor of ten. Also, on May 10, 1977, the concentration of nauplii at the same station was low.

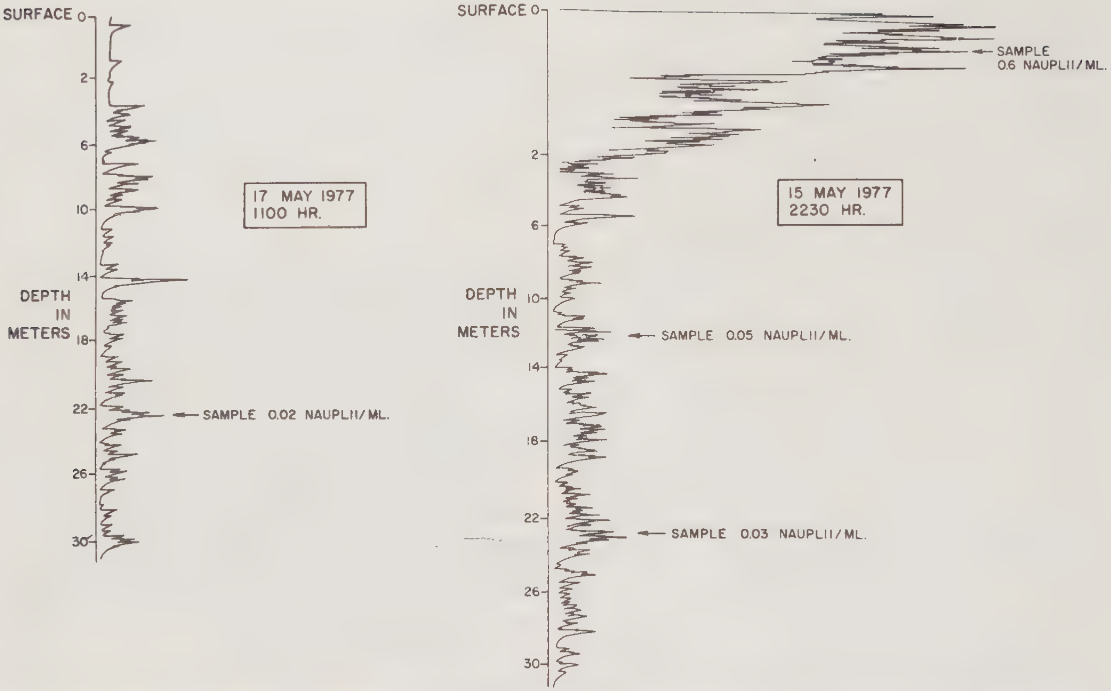


Figure 4. Chart records of vertical distribution of copepod nauplii collected in Austnesfjorden, Norway, by the *in situ* device for sensing and collecting microplankton.

In Austnesfjorden, we found the device to be very effective in identifying and collecting discrete samples of seawater from regions of high plankton density. Seawater collected in this manner was used for bioassay experiments with cod larvae to determine feeding thresholds, rates, and food preferences (Ellertsen et al. 1981).

The effectiveness of this technique depends on local conditions. For instance, during two cruises in the New York Bight, rough weather hampered attempts to identify plankton patches. It is hard to assess how much this was caused by the dispersal of patches due to mixing on the upper layers, and how much was due to the ship's movement, which made it impossible to sample discrete points in the water column.

The effectiveness of the device can also be reduced by interfering particles in the water. During one cruise off the coast of Long Island, New York, high concentrations of a large phytoplankton *(Ceratium tripos)* masked the presence of micronauplii.

SUMMARY

The device for sensing and collecting microplankton was found to be effective during 45 days of sea trials. Effectiveness depends on local conditions such as sea state, weather, and the presence of interfering particles like large phytoplankton or detritus that can mask the presence of micronauplii.

This device has been used successfully to collect discrete samples of seawater from regions of high nauplii density for use in larval fish bioassay experiments. To our knowledge, the highest concentration of nauplii (0.6/ml) ever found at sea was collected with this device.

Laboratory tests indicate that zooplankton nauplii less than approximately 560 μm could not avoid the influent currents of this device. Also, there was no evidence of injury to nauplii during pumping, and smearing of the sample during collection was minimal.

An old Coulter Counter Model A was modified for this application because one happened to be available. However, an inexpensive pulse height analyser could also be used for this purpose.

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ANNEX 4

Microcomputers and Fisheries

by

Robert A. Skillman
Southwest Fisheries Center, Honolulu Laboratory
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
Honolulu, Hawaii

1. INTRODUCTION

Research and management relating to living resources require extensive data bases. Because of the multiplicity of species, fishing gear and participating nations, fisheries research and management activities may require much more data than any other resource management area. This situation led fisheries scientists and managers to embrace good record-keeping practices and to apply statistical survey procedures. The resulting large depositories of data contributed materially to the development of quantitative techniques for fishery stock assessment in the early 1900s. The ever-increasing size of the data sets created problems in processing and managing them in a timely and cost-efficient manner. With the development of the computer during World War II and its commercial availability shortly thereafter, a new tool became available for managing and processing these large fisheries data sets.

Fisheries workers adopted this new tool, learned high-level programming languages, such as FORTRAN, to process their data, and proceeded in an effort to gain access to ever bigger, more powerful mainframe computers.

In the middle to late 1970s, developments occurred in the computer field that are only now being recognized and adopted to any great extent in fisheries. These developments include: (1) maintenance of data sets in mass storage devices (disks) attached directly to computers rather than on magnetic tapes to facilitate speedy access for updating or analysis; (2) interactive rather than batch processing; (3) availability of smaller computers called minicomputers; and (4) time-sharing of processing resources on a mainframe computer.

Two recently occurring computer developments are not, except for a few instances, being used in fisheries. One involves a concept called distributed processing, where two or more small computers perform site specific processing but are linked together in a network for sharing of data bases and, sometimes, the processing power of a central, large computer. The second event, which is the subject of this paper, involves the development of the general purpose microcomputer.

In this report, I will describe the general purpose microcomputer, discuss its capabilities, compare its performance specifications to some minicomputers, and finally present some fisheries applications of microcomputers.

In discussing computers, it will be necessary to use words and terminology unfamiliar to most fisheries workers. To make matters worse, the computer field is rich in jargon that is evolving as rapidly as the field itself. I will attempt to avoid as many of the specialized terms as possible but the use of some will be necessary. To facilitate our communication, I have included a short glossary (Appendix 1), which I extracted mostly from McGlynn (1979) and Popular Computing (1981).

2. THE MICROCOMPUTER

2.1 Some Definitions

What is a microcomputer? And, what makes it different from the computers we fisheries scientists have been using all these years? The glossary presents the text book definition, but further explanation seems in order.

A computer system, besides essentially being an assemblage of machines whose purpose is to process information, is made up of several devices - some for inputting information, some for storing if, some for outputting it, and one for processing it. The latter is generally called the central processing unit (CPU). It is the heart of the computer and is purely electronic, not electro-mechanical. The CPU is in turn made up of an arithmetic logic unit, some registers for temporary storage of data, instructions and address (much like the registers on a calculator), an instruction decoder and timing unit (determines what part of the CPU is instructed to do something and when), sometimes a clock, a memory and input-output controller (for communicating with random access memory and the input-output interface), and communication wires (called buses; for transmitting data, addresses and control instructions).

Large mainframe computers or maxicomputers, for example the IBM[1/], Univac and Burroughs machines which have been used for so many years, are products of the electronics industry. In these machines, the CPU is made up of separate electronic units linked together inside a cabinet to accomplish each of the functions of the CPU given above. These units of boxes have gotten smaller over the years, but they are still separate electronic units. In minicomputers, a great advancement was made in miniaturization so that the arithmetic logic unit, the registers, and the instruction decoder and timing unit could be placed together on an electronic board. These electronic boards not only take less space than the electronic units of the maxicomputers, but they are cheaper to manufacture and are more dependable.

Microcomputers are products of the semiconductor industry and are fundamentally different from both mini- and maxicomputers. In this case, all of the processing functions of the CPU are placed together on a single silicon chip smaller than your fingernail. Hence, the phrase "computer on a chip". Technically, the silicon chip is a microprocessor. This chip is placed on an electronic board along with part or all of the random access memory, the clock, the input-output interfacing unit, and extensions of the communication buses. Hence, the entire CPU can now reside on a single electronic board although frequently part of the random access memory is placed on a separate board. This arrangement is cheaper to manufacture and more dependable than that used in the minicomputer.

Thus, the basic difference among maxi-, mini- and microcomputers is the electronic architecture. What about using processing capacity as a means of defining these types of computers? In general the maxicomputers are capable of doing more processing faster than mini- or microcomputers. However, as minicomputers improved, they became capable of performing the same work in less time and at less cost than smaller, less capable maxicomputers. Hence, the more efficient minicomputers have displaced the less efficient maxicomputers from the market place. Similarly, advances in microcomputers have resulted in the displacement of the smaller, less capable minicomputers. Today, a microcomputer costing US$ 2 000-3 000 is more powerful, faster and more compact than the first computer costing millions of US dollars. The processing power of each of the computer types is advancing rapidly and will continue to do so for the foreseeable future; hence, processing power is not a good means for characterizing types of computers.

1/ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

2.2 Some Early Uses

The microprocessor was originally created to handle routine, set tasks commonly used in controlling manufacturing processes. It was only later that the microcomputer, encompassing the microprocessor, was used for manufacturing, business, and scientific applications. Some of the first applications of microprocessors in science were to interface between laboratory or field instruments and some recording device or a computer. In fisheries and oceanography, microprocessors are used with instruments measuring temperature, conductivity, pressure, current, and weight. In such instruments, they can be used to control the rate at which the sensory instruments operate, to convert the devices' analog signals to digital signals for subsequent analysis on computers, and to filter, smooth or average data generated by sensory instruments. They calculate salinity from temperature, pressure, and conductivity readings and the position of ships from satellite signals (see Mini-Micro Systems 1979 for a description of a forerunner to the off-the-shelf satellite navigation instruments that are available today). They can be used to estimate the potential amount of naturally occurring fish food by counting free-fall particles (Lasker and Brown, 1978).

Increasingly, microcomputers, rather than microprocessors, are being built into laboratory and field instruments because they can be programmed to handle variable situations including the changing of work performed by the instruments in response to changes in the factors being measured. For this reason, microcomputers are being employed in oceanographic data buoys (Lobecker et al., 1978), in unmanned underwater vehicles (Marine Industrial Advisory Service, 1980) and echo-sounder integration systems to estimate fish abundance (Kanemori and Ehrenberg, 1978; Iida and Susuki, 1980). Although these machines are programmable, they are essentially dedicated to one particular kind of task.

2.3 The General Purpose Microcomputer

Of greater significance to fisheries workers today is the availability of powerful, but relatively inexpensive, general purpose microcomputers. Sometimes they are called desk-top computers, but the largest reside in cabinets. Most are 8-bit machines (that is, they use eight binary digits consisting of either 0s or 1s to represent numeric data, alphabetic letters, and special characters), although 16-bit machines are becoming more common. Some of these microcomputers are capable of supporting several users whereas others only one user. The latter are called personal computers.

In the following paragraphs, I will state some of the advantages of personal and multiuser microcomputers, comment on available computer programming languages, describe several commercially available computer program packages, and end with some brief material on communicating with other computers and sensory instruments.

The great advantage of a personal computer is that it is available for immediate use at any time for nearly any application the user wishes. Unlike users of large computers, the personal computer user does not contend with slow response time of inability to gain access to the computer because too many users are on the system. Neither is the user of a personal computer subject to processing expenses or operator-imposed restrictions associated with large computers.

The multiuser microcomputer also has several advantages. Since such computers are usually dedicated to a small group of associated users rather than to some organization-wide support group, they are available for use at the convenience of the group. Computer programs and data sets can easily be shared. Peripheral devices, such as disks, a painter, and a graphics plotter can be shared, thus lowering the overall cost. Of course, only one user can utilize these paripherals at any one time.

BASIC is the most commonly used programming language, but many microcomputers can be programmed in several other high-level languages such as FORTRAN, COBOL and PL/I. In addition, several new structured programming languages, for example, Pascal, are becoming available for microcomputers. High-level languages allow the user to program the computer to perform almost any type of processing task imaginable.

Many new computer programs (or software) are becoming commercially available that significantly increase the utility of these machines to fisheries workers. Previously, software for data entry, file management and data-base management were available only on mainframe computers. Without such software for microcomputers, it was very laborious to enter data and manage the data sets for subsequent analysis. Now, there are several commercially available software packages for microcomputers that allow the user to set up data entry formats, manage individual data sets, or combine data sets or elements from several data sets for subsequent analysis. While these currently available packages are not as powerful as those for mainframe computers, they have significantly increased the usefulness of the microcomputer and the productivity of its users. With more powerful 16-bit microcomputers becoming available, this situation should improve.

Some statistical software packages exist for performing simple parametric and nonparametric analyses including time-series analysis. However, these packages generally are not very powerful because of limited machine memory, language-based restrictions on the number of significant digits that can be carried in calculations, and poor data entry and management procedures. Very few quantitative fisheries applications have been programmed onto microcomputers, but is should be fairly straight forward to do so. Again, with the entry of more powerful 16-bit microcomputers, more sophisticated statistical software should become available, and it should be possible to program all but our most complicated stock assessment methodologies onto these computers.

Most of the statistical software also have the ability to plot the data used in the analyses and the results from the analyses. Needs in the business world have resulted in software capable of producing pie charts and bar graphs, in color if you wish. Needs in the automotive, aircraft, and communication industries have resulted in the development of graphics software capable of displaying three dimensional charts, expanding views of selected areas of a display, rotating figures, and changing the angle of view. Thus, the available software is probably capable of handling any fisheries application; but the technology must be transferred to fisheries. Graphic representations of data can be displayed on monochrome or color video terminals or can be sent to graphics printers or plotters. The cost of these devices, particularly graphics printers, has decreased substantially the last couple of years, thus making them available to many more users. Relatively inexpensive color graphics printers are now available.

The microcomputer industry has created a unique type of software that has not as yet been implemented on larger computers. This software allows the user to set up a grid of columns and rows that can be mathematicaly interrelated according to the user's specifications. If the user wishes to see the consequences of changing some of the numbers entered into the spread sheet, he merely enters the new numbers and the rest of the table is recalculated. Thus, simple simulating can be programmed in minutes rather than hours using regular high-level languages.

The last type of microcomputer software that I will discuss, word processing, has tremendous utility in fisheries. Although this software accomplishes a task that is technically not part of fisheries or any science, word processing can reduce the time spent writing scientific documents. To produce this paper, I outlined what I wanted to say, collected information from the literature to supplement what I wanted to say, prepared a more detailed outline, and then sat down in front of a microcomputer and wrote the paper. The software allowed me to edit various sections, make insertions, and move whole sections around before I was satisfied with the document. When I passed the text file containing the document to the secretarial staff for finalization, they did not have to decipher cross outs, insertions, and arrows pointing in various directions. When they finished their work, I did not have to check for introduced typing errors. It is much easier and faster to prepare documents using word processing than by any other method. Word processing can be accomplished on micrcomputers, dedicated word processors, or mainframe computers, but these latter devices are less available to individual scientists.

Devices called modems and the software to support them allow the user of a microcomputer to communicate with other microcomputers or with mainframe computers. This facility essentially turns the microcomputer into a terminal which can then be used to transfer data sets to or from a mainframe computer and to conduct analyses directly on the larger computer. In addition, software is available for some microcomputers making it possible for them to function as a remote job entry station to a mainframe computer (27 80/37 80 protocol emulator). The capability of a microcomputer to emulate a terminal or a remote job entry station is extremely useful because it allows the microcomputer user to manage and process very large data sets on the mainframe computer and then use the microcomputer to process compacted data retrieved from the larger computer.

Most general-purpose microcomputers have the ability to interrupt ongoing processing and interrogate scientific measuring instruments, store or process the data received, and then return to the other task it was performing. Thus, the microcomputer can be used to control or conduct experiments while still being used as a data processing computer.

2.4 Comparing Microcomputers and Minicomputers

In the material presented above, I called the microcomputer a powerful tool and discussed some of its capabilities in terms of available software for data processing. To put things into perspective, I will compare specifications and costs for the basic hardware comprising a minicomputer and a microcomputer. For this comparison, I will use two tables listing the features of several minicomputers that were prepared by the International Commission for the Conservation of Atlantic Tunas (ICCAT) in 1978 and the Food and Agriculture Organization (FAO) Project for Tuna Management in 1980. The minicomputer procured by the Skipjack Assessment Programme of the South Pacific Commission (SPC) is included in these tables. The microcomputer used in the comparison is produced by Integrated Business Computers, a relatively small manufacturer in the US. Although this is a sophisticated system, it is not unique in the United States, Japan or Europe.

In 1978 the SPC acquired a Hewlett-Packard (HP) 1000 model 45 minicomputer to support their tagging activities. At the time, this computer represented the state of the art for mid-range minicomputers. In the same year, ICCAT prepared a paper comparing the capability and cost of several minicomputers (including the HP 1000) to the costs of time-share services from Computer Sciences Corporation's Information Network (Nordstom and Miyake, 1978). The hardware specifications and costs for the minicomputers are reproduced in Table 1. In 1980, FAO's Project for Tuna Management prepared a similar table comparing the features and costs of minicomputers for consideration by the tuna committees of the Indo-Pacific Fisheries Commission and the Indian Ocean Fisheries Commission (Skillman, 1980). By today's standards, these minicomputers (Table 2) no longer represent the state of the art, and they fall into the lower range of the capability of minicomputers.

It can be seen from Tables 1 and 2 that the cost of these systems has decreased substantially. In 1978, the cost of the basic HP system was nearly US$ 100 000. The least expensive system, the IBM, cost about US$ 88 000; the most expensive, Digital, cost US$ 106 000. By 1980, HP had become the least expensive system, costing only about US$ 58 000. The most expensive was the FACOM at over US$ 91 000.

From Table 3, it can be seen that the IBC microcomputer compares favorably with the minicomputers listed in Tables 1 and 2 in terms of central processor memory (its maximum memory is significantly less than the largest of the minicomputers, however), cycle time (a measure of internal speed; significantly faster than any of the minicomputers), and disk-storage capacity. The manufacturer's specifications did not give the density of the 9-track tape drive, but it is probably no more than 800 bits per inch (bpi), which is the same for the minicomputers listed in Table 1. Also, the disks may be slower than those used with minicomputers. Specifications are not the whole story, but this 8-bit microcomputer does compare reasonably well with the minicomputers listed.

For a number of years now, the 8-bit microcomputer has been dominating the market; however, the microcomputer field is undergoing a revolution because of the introduction of the 16-bit microprocessor. Today there are at least 20 microcomputers using these more powerful microprocessors. These new microcomputers are not only faster, but more importantly they can directly address much more memory (1.0 Mbytes or more as compared to 64 Kbytes). All or most of the minicomputers listed in Tables 1 and 2 are 16-bit machines. As the manufacturers of 16-bit microcomputers improve their products and make them more sophisticated, the 16-bit microcomputers will undoubtedly displace minicomputers of the level discussed here. In addition, two manufacturers have announced 32-bit microprocessors, and one indicated that manufacturing would start in 1983.

3. RECENT FISHERIES APPLICATIONS USING MICROCOMPUTERS

General purpose microcomputers are being used in fisheries to an increasing extent, including the Central and Western Pacific. As an illustration of this, I will present below the three recent applications.

3.1 Western Pacific Fisheries Information Network

With the passage of the Magnuson Fishery Conservation and Management Act in 1976, Federal and State fisheries managers have experienced an increasing need for data on fisheries resources in the US Fishery Conservation Zone. Accurate data are needed on a timely basis for management decisions and the preparation of fishery management plans. Managers and scientists in the National Marine Fisheries Service (NMFS), the Western Pacific Regional Fishery Management Council, and state and territorial fisheries agencies have encountered problems due to the lack of a historical data base, unavailability of existing data for analysis, legal constraints for data exchange, lack of data standardization, and inadequate procedures for data collection. The Southwest Fisheries Center started the Western Pacific Fishery Information Network project to solve these problems[1/]. Specifically, the purpose of the project is to (1) enchance and modernize the existing systems for fisheries information management and data collection; (2) develop and implement new systems for information management and data collection; (3) establish both central and distributed, computerized data bases; and (4) establish a communication network among state, territorial, and Southwest Fisheries Center data collection and processing groups for access to, and exchange of, the computerized data bases. The agencies included in the network are, in addition to the Honolulu Laboratory of the Southwest Fisheries Center, the American Samoa Office of Marine Resources, the Northern Mariana Islands Department of Natural Resources, Guam Division of Aquatic and Wildlife Resources, and Hawaii Division of Aquatic Resources.

The network is a distributed computer system consisting of a central minicomputer and satellite microcomputers (Figure 1). The central minicomputer system consists of a Digital Equipment Corporation PDP 11/70 accessed on a time-share basis using video display terminals or a microcomputer. The distributed microcomputer systems consist of Apple II Plus microcomputers each with twin 5-1/4 inch (13.3 cm) floppy disk drives, a dot matrix printer, and a video screen. Micromodems are included with the microcomputers located at the Honolulu Laboratory and the Hawaii Division of Aquatic Resources.

A similar network is being set up by the National Marine Fisheries Services' Southeast Fisheries Center for essentially the same purpose. This network will involve all the States in the southeastern US and will include data on fisheries resources under US jurisdiction in the Gulf of Mexico, the Caribbean, and off the southeast Atlantic coast.

3.2 Resource Assessments in the Indo-Pacific Region

The International Center for Living Aquatic Resources Management (ICLARM) is conducting several studies involving the assessment of demersal and pelagic fish stocks in Southeast Asia. Recently, Pauly (1981) indicated that they are establishing a microcomputer-based

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[1/] Hamm, D.C., Preliminary description of the Western Pacific Fishery Information Network.
1982 Admin.Rep.Southwest Fish.Cent.NOAA/NMFS, (H-82-2):11 p.

system for filing trawl survey data on fisheries in the region and for their analysis by local scientists. In this same paper, Pauly also announced the availability of microcomputer software to calculate von Bertalanffy growth parameters and catch curves from length-frequency data.

3.3 Laboratory Research on Tuna in Hawaii

At the Kewalo Research Facility of the Honolulu Laboratory, microcomputers are being employed in experiments involving physiological parameters, environmental variables such as temperature, feeding preferences and rates, and electromagnetic fields. The microcomputers are interfaced with sensing devices to determine the movement and other bahavioural responses of captive animals being subjected to various experimental procedures. The microcomputers are programmed to analyse the bahaviour of the experimental fishes and alter the experiment in response to the fish's behaviour. In this way, the experimental animals' preference for environmental factors such as temperature have been determined. The ability of skipjack tuna, Katsuwonus pelamis, and other tuna to sense changes in the earth's electromagnetic field, is being investigated to determine their ability to use this environmental cue for migration.

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APPENDIX 1

Glossary

Analog. In the computer field, the use of electric voltages as physical analogues of numerical variables.

Architecture. Organizational structure of a computing system, mainly referring to the CPU or microprocessor.

BASIC. The most popular high-level language used on microcomputers. Short for "Beginner's All-purpose Symbolic Instruction Code".

Bit. An abbreviation of "binary digit"; single characters of a binary number, either 0 or 1 in the case of computers.

Byte (B). A sequence of n bits operated upon as a unit is called an n-bit byte. The most frequent size is 8 bits. KB stands for 1 024 bytes, and MB stands for 1 megabyte.

Bus. A group of wires that allow memory, CPU, and input/output devices to exchange data.

Clock. In a small computer, a device that sends out timing pulses to synchronize the actions of the computer.

COBOL. Short for "Common Business-Oriented Language"; a high-level language.

Computer Program (Program). A collection of instructions properly ordered to perform a particular task.

CPU (Central Processing Unit). That part of a computer system that controls the interpretation and execution of instructions. In general, the CPU contains the following elements: arithmetic-logic unit, timing and control, accumulator, scratch-pad memory, program counter and pointer stack, instruction register and decoder, parallel data and input/output bus, memory and input/output control.

Data Base. The entire collection of information available to a computer system. Or, a structured collection of information as an entity or collection of related files treated as an entity.

Data Base Management System (DBMS). Facilities for creating and maintaing a large, organized, structured collection of data and providing means for producing various types of predetermined reports based upon interrogation of the data base.

Data Set. A collection of data records, with a logical relation of one to another.

Digital. Of or pertaining to numerical bits.

Disk. A round piece of magnetic-coated material used to store data with greater density, speed, and reliability than with magnetic tapes. Floppy disks have thin 5-1/4 inch (13.3 cm) or 8 in. (20.3 cm) disks. Hard disks are thicker and can be much larger.

FORTRAN. A high-level language generally for scientific use, expressed in algebraic notation. Short for "Formula Translator".

Hardware. Physical equipment forming a computer system.

High-level Language. User-oriented programming languages using letters, symbols, or English-like text from which are generated codes the computer understands. FORTRAN, COBOL, and BASIC are three commonly used high-level languages.

Input-Output (I/O). General term for the process of communicating between the computer and external devices; or the data involved in that communication.

Mainframe Computer. A large-scale computer such as the IBM System 370 maxicomputer of a Digital VAX 11/370 minicomputer.

Memory. That part of a computer that holds data and instructions. Each instruction or datum is assigned a unique address that is used by the CPU when fetching or storing the information.

Microcomputer. A computer whose CPU is a microprocessor. A microcomputer is an entire system with microprocessor, memory, and input-output controllers.

Microprocessor. Frequently called "computer on a chip". The microprocessor is, in reality, a set of one, or a few, large-scale integrated circuits capable of performing the essential functions of a computer CPU.

Modem. Short for Modulator/demodulator. An electronic device that allows computer equipment to send and receive information through telephone lines.

Network. An interconnected group of computer systems, terminals, or communications facilities for sharing of data bases or computer processing resources.

Peripheral Device. Equipment that is external to the computer itself, for example, disks and printers.

Pascal. A high-level, structured programming language named after the 17th century French mathematician Blaise Pascal.

PL/I. A high-level, structured programming language combining features from COBOL, FORTRAN, and other languages. Short for "Programming Language One".

Software. Computer programs.

Terminal. An input-output device that interfaces between the human operator and the computer system, for example, a teletype or a video display terminal.

Video Display Terminal (VDT). A terminal containing a screen for viewing data entered into or received by the terminal. A cathode-ray tube is most commonly used resulting in the acronym CRT.

Table 1. Comparison of ICCAT's minicomputer performance and cost[1] (from Nördstrom and Miyake, 1978)

System models recommended	DIGITAL PDP-11 Model-34A	US$	HEWLETT-PACKARD 1000 Model 45	US$	IBM Series 1 Model E	US$	TEXAS INSTRUMENTS DS 990/10 Model 4	US$
HARDWARE								
Processor								
Memory	128K bytes		120K bytes		128K bytes		256K bytes	
Speed (cycle time)	725 n.s.				660 n.s.		725 n.s.	
Console	Printer (30 cps)		Screen		Screen		Screen	
I/O Devices								
Disks	14MB x 2		9.8MB x 2		64MB x 1		5MB x 4	
Av. access time	50.5 MS		33 MS		36 MS		35 MS	
Diskette magazine unit	—		—		28 MB		—	
Tape unit	800 BPI		800 BPI		—		800 BPI	
Printer	180 cps x 2		180 cps		150 l.p.m. (approximately 200 cps)		150 cps x 2	
HARDWARE COST:		103 367		—		77 271		91 560
SOFTWARE								
FORTRAN IV	Available		Available		Available		Available	
Utilities and sort	Available		Available		Available		Available	
SOFTWARE COST:		2 338				10 656		5 550
TOTAL PRICE		105 705		99 989		87 927		97 110
OPTIONAL								
Processor								
Memory	Up to 248KB		Up to 2MB (by unit of 128K)	8 071/128K	Up to 256KB	11 743	Up to 2MB	
Card reader	300 c/m	9 500	600 c/m	10 291	Not available		400 c/m	7 800
V D U (Screen)			Available	5 246	Available		Available	
Plotter	Not available[2]		280 x 400 mm	7 743	Not available[2]		Not available[2]	
Software (Data base managing system)	DATATRIEVE-11	6 493	IMAGE/120	4 571	Not available at present		Available	3 000

[1] Estimates for prices are valid for October-November 1978. Prices are given in pesetas and converted into US$.

[2] Any makes can be adopted.

Table 2. Comparison of minicomputer performance and cost (from Skillman, 1980)

System/Models Specifications	DEC PDP-11/34A	US$	FACOM V-830	6/ US$	HEWLETT-PACKARD HP 1000, Mod 45	US$	IBM Series 1, Mod E	US$	Texas Instruments TI990/10 Model 4	US$	Wang Model 2200 VS	US$
Basic configuration												
Central processor												
Memory	128K	n/c	262K	n/c	128K	n/c	128K	27 200 (operating system)	256K	n/c	128K	n/c
Speed (cycle time)	725 n.s.		400 n.s./2B		420 n.s.		660 n.s.		725 n.s.		660 n.s.	
Console	printer 30 cps	n/c	screen	n/c	graphics screen	n/c		2 000 1 700	screen	n/c	screen	n/c
Cost		54 000		45 700		43 500		30 900		34 500		21 800
Peripherals												
Main storage	disk 28MB (x2)	n/c	disk 40MB disk 40MB(x4)	n/c 9 400	disk 19.6 MB (x2)	n/c	64MB x 1	10 700	disk 5MB (x4)	7 800	disk 75MB (x4)	19 000/ unit
Backup storage	tape 1600bpi	17 000	tape 1600bpi	22 800	tape 800bpi	10 750	tape	17 500	tape 800bpi	10 000	tape 800/ 11600bpi	16 100
Printer	180 cps(x 2)	7 400	180 cps	9 582	180 cps	4 000		8 600	150 cps(x 2)	5 500	220 cps	10 350
Cost		24 400		41 782		14 750		36 800		23 300		45 450
Software												
FORTRAN IV	available	800	available	75/mo.	available	n/c	available 2/	870	available	1 000	available	n/c 3/
Utilities and sort	available	n/c	available	165/mo.	available	n/c	available	720	available	2 500	available	n/c
COBOL	available	?	available	75/mo.		n/a	available	870		n/a	available	3 450
Cost		800				0		2 460		3 500		3 450
Total cost		79 200		91 262		58 250		70 160		61 300		70 700
Options												
Memory up to	256K	4 000	512 KB	3 600/ 128KB	2 MB in 128K	3 500/ 128K	256K	1 510/ 16KB	1 MB	575/ 4Kwords	512K for VS 2 048K for VS 100	8 500/ 128K 10 350/ 128K
Card reader	300 c/m	7 000	600 c/m	17 030	600 c/m	6 375		n/a	400 c/m	5 200		n/a
Video display screen	available	2 200	available	3 862	available	3 500		n/a	available	2 000	available	2 900
X-Y plotter		n/a		n/a		2 600		n/a		n/a	not now available	
Data Base Software		4 500	available	200/mo.		3 000		n/a		2 000	available 4/	n/c
Word Processor Software											available 5/	3 000

1/ Cost estimates were quoted by west coast vendors in U.S.A. and may vary withthe site chosen in Indo/Pacific area.

2/ PL/1 language is also available.

3/ BASIC and PL/1 languages also available; Assembler and one higher order language included with price of system and each additional language cost $3.450.

4/ An advanced DBMS is available for $17 250.

5/ Word processor terminal (CFT) cost $4 376.

6/ CIF Manila

Table 3. Specifications, performance capability, and cost of an IBC Ensign Model E-1256 microcomputer

Specifications	Values	Cost US$
Basic configuration		
Central processor		10 850
Memory	256K	n/c
Speed (cycle time)	120 nsec	--
Console	Video	1 300
Subtotal		12 150
Peripherals		
Main storage	2, floppy disks (2.4MB	n/c
	Winchester disk (50MB)	8 200
Backup storage	9 track tape drive	2 250
Printer	150 cps	1 695
Subtotal		12 145
Software		
Basic	Available	290
COBOL	do	580
FORTRAN	do	350
Pascal	do	430
PL/I	do	460
Operating system cp/M	4 different systems	300
Subtotal		2 410
Total		26 705
Options		
Memory up to	768KB	4 200/256KB
Card reader	Not available from manufacturer	
Video display terminals	3 models	800 to 1 300
X-Y plotter	Available from other vendors	
Data base software	do	
Word processor software	do	

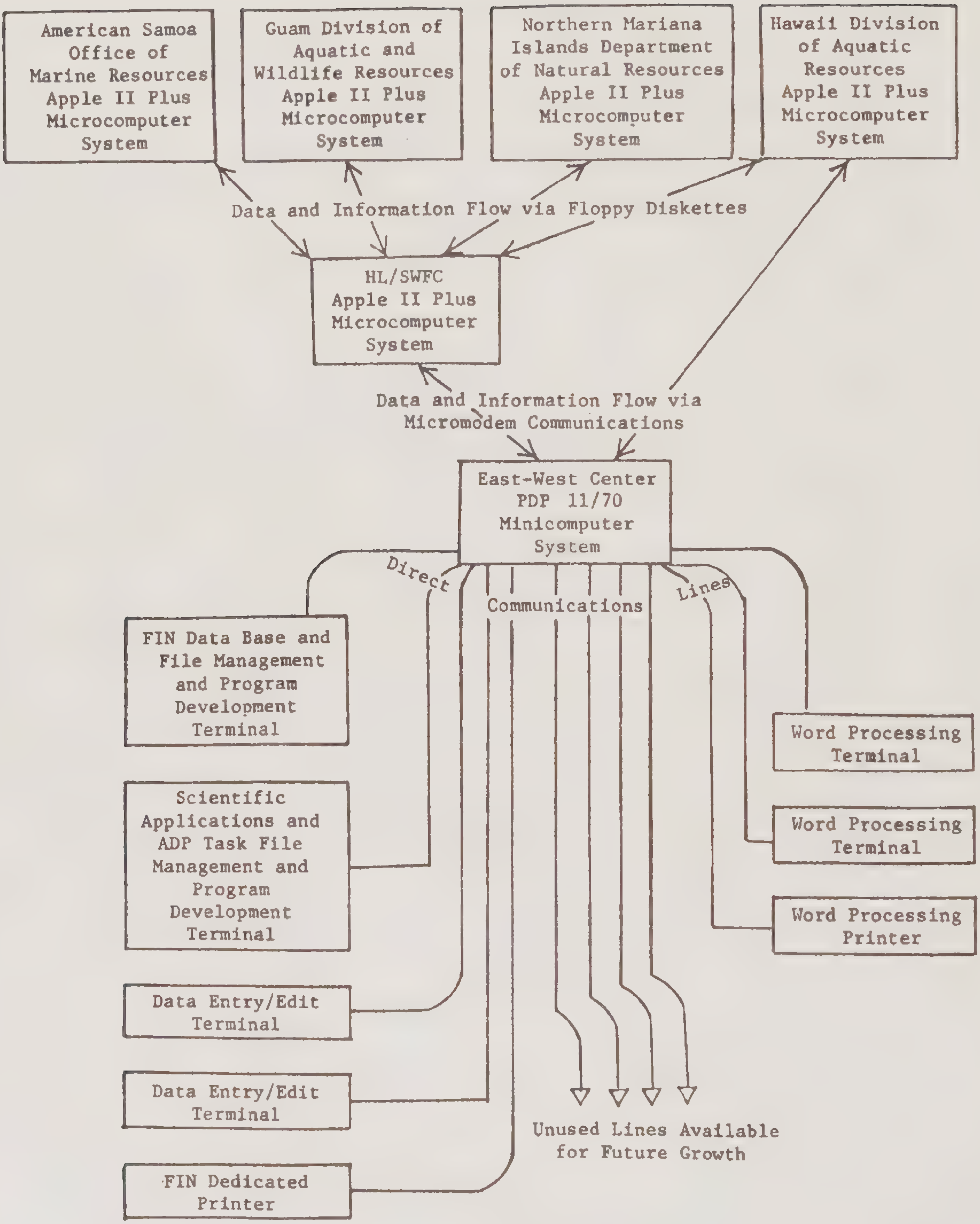
American Samoa Office of Marine Resources Apple II Plus Microcomputer System
Guam Division of Aquatic and Wildlife Resources Apple II Plus Microcomputer System
Northern Mariana Islands Department of Natural Resources Apple II Plus Microcomputer System
Hawaii Division of Aquatic Resources Apple II Plus Microcomputer System
Data and Information Flow via Floppy Diskettes
HL/SWFC Apple II Plus Microcomputer System
Data and Information Flow via Micromodem Communications
East-West Center PDP 11/70 Minicomputer System
Direct Communications Lines
FIN Data Base and File Management and Program Development Terminal
Scientific Applications and ADP Task File Management and Program Development Terminal
Data Entry/Edit Terminal
Data Entry/Edit Terminal
FIN Dedicated Printer
Word Processing Terminal
Word Processing Terminal
Word Processing Printer
Unused Lines Available for Future Growth

Figure 1. The WPACFIN hardware configuration (see text footnote 2)

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Primary production and the anchovy population in the Southern California Bight: Comparison of time series[1]

Paul E. Smith
National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038

Richard W. Eppley
Institute of Marine Resources A-018, University of California, San Diego, La Jolla 92093

Abstract

Two new time series for the Southern California Bight are presented: anchovy biomass, 1951–1979, and primary production, estimated for the years 1920–1979 from 15 cruises conducted between 1974 and 1979. Annual and longer term averages show little relationship to each other except that values for both were low in the climatically warm water years 1957–1958. The primary production time series is similar to two existing time series: CalCOFI zooplankton in the bight and microplankton in Santa Monica Bay, 1951–1966. Thus estimated primary production does reflect the carrying capacity of these waters for lower trophic level consumers.

Seasonal averages of anchovy larvae are highest in the winter and spring quarters when primary production is increasing. Interannual variation was pronounced in both seasonal average primary production and seasonal average abundance of anchovy larvae. About 50% of the variation in number of anchovy larvae was explained by variation in primary production in the same quarter and zooplankton standing stock three quarters earlier. In 1966, the year of maximum anchovy abundance, the energy expended in anchovy egg production was equivalent to about 1.8% of primary production. The anchovy ration was about 18% of primary production. The ratio of zooplankton biomass to primary production was highest in years when anchovy biomass was greatest.

The eastern margins of the oceans are regions of high productivity (Cushing 1969) and the California Current is one of the major sites of long term study of eastern boundary current and upwelling systems. Gulland (1971) stated that the ultimate controls of fish abundance were primary productivity and ecological efficiency. Murphy (1966) described the oceanic conditions which lead to high abundance of plankton and planktivorous fishes and Lasker (1970) provided a lengthy time series of the caloric requirements of a single major fish population—the Pacific sardine. The coincidence and alternation of massive populations of planktivorous fishes in the eastern boundary current regions remain one of the major questions in marine ecology.

We here examine functional relationships between primary production and anchovy population using two lengthy time series: estimated Southern California Bight primary production (1920–1979) and estimated biomass of that portion of the central subpopulation of the

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[1] Supported by U.S. DOE contract DE-AM03-76SF00010.

northern anchovy, *Engraulis mordax* (Girard), which inhabits the Southern California Bight region (1951–1979), and we compare these new time series with zooplankton abundance previously reported for the region. To what extent does primary production set limits on anchovy production? What other environmental and biological features may ultimately control the population size of the anchovy?

Time series have many uses and provide a valuable component in the study of marine ecosystems. At the descriptive level they can exist as records of species succession over time or as trends in environmental conditions. They can establish the magnitude of variability on temporal (e.g. Robinson 1970) or spatial scales (Blackburn 1973; Larrance 1971) of interest. They are useful in developing inferences on the regulation of populations through environmental change or overfishing, as in developing methods of predicting fish recruitment from the environmental conditions during larval drift (Cushing 1975, p. 236). In principle, time series of populations at different trophic levels can be used to examine material and energy flow in food webs and the variability and range of values of transfer efficiencies. It remains to be seen whether we can recognize from time series of changes in populations such things as interactions between species independent of changes due to climate-related environmental change or fishing intensity, since the latter are strong signals in the records.

The apparent spawning biomass of the central stock of the northern anchovy increased for about 15 years, reaching in 1966 a standing stock 30 times that in 1952. Radovich and MacCall (1979) fit the logistic equation to this increase; the two parameters of interest from their analysis are the maximum rate of population increase and the maximum carrying capacity of the environment. For the central stock, their estimates of the parameters are 0.3 million tonnes per year increase at an intermediate spawning biomass of 2 million tonnes and a maximum carrying capacity of ca. 4 million tonnes. A large fraction of the population is likely to be made up of nonspawners, thus the impact of the anchovy on its environment may be considerable and greater than estimated by the spawning biomass. Reproduction of the central stock of anchovy failed in 1974 and 1975, and the spawning biomass fell by 1976 to about 1 million tonnes. It began a small recovery to about 1.8 million tonnes in 1979 (Stauffer: SW Fish. Center Admin. Rep. LJ-79-22).

The anchovy is omnivorous, filtering and biting zooplankton and filtering phytoplankton. Loukashkin (1970) found far more zooplankton than phytoplankton in the stomachs he examined and concluded that large copepods and euphausiids were the most important food items. O'Connell (1972) analyzed the feeding behavior of captive anchovy schools and concluded that biting was their most efficient method of feeding but that biting the larger zooplankters could be usefully augmented by filtering small zooplankters and phytoplankton. Available studies suggest strongly that the anchovy is omnivorous and feeds on carnivores, other omnivores, herbivores, and directly on phytoplankton.

The northern anchovy is a schooling fish, thus its impact is not applied evenly throughout the habitat (Smith 1970; Hewitt and Smith 1979; Koslow 1980). The 4-million-tonne central stock (Fig. 1) may be distributed among 100 school groups, 9 km in diameter (Fiedler 1977) with 15 schools per square kilometer within the groups (Smith 1977). Analysis of pictures from free-fall cameras (Graves 1977) indicated that anchovy form schools at densities up to $366 \cdot m^{-3}$; the average concentration estimated from purse seine sets was $15\ kg \cdot m^{-2}$ (Hewitt et al. 1976) (range, $0.1–125\ kg \cdot m^{-2}$).

Fish have been considered in studies of production and nutrient cycles. Ryther et al. (1971) stated that an average annual rate of primary production of the order of $1{,}000\ g\ C \cdot m^{-2}$ is needed to satisfy Peruvian anchoveta (*Engraulis ringens*) production. Whitledge and Packard (1971) found

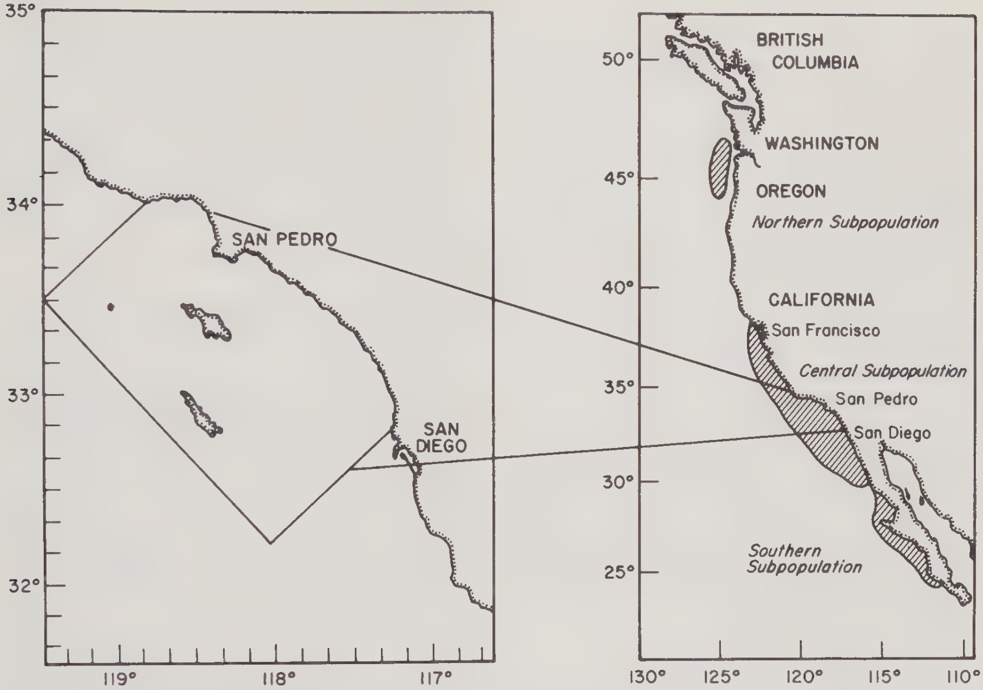
35°
34°
33°
32°
SAN PEDRO
SAN DIEGO
119°
118°
117°
BRITISH COLUMBIA
WASHINGTON
OREGON
Northern Subpopulation
CALIFORNIA
San Francisco
Central Subpopulation
San Pedro
San Diego
Southern Subpopulation
50°
45°
40°
35°
30°
25°
130°
125°
120°
115°
110°

Fig. 1. Left—survey boundary for primary production measurements in Southern California Bight. Right—subpopulation distributions of northern anchovy, *Engraulis mordax*.

a local enrichment of 40% of ammonium-N in a surface water sample taken in a Peruvian anchoveta school. Dugdale (1976) emphasized the role of the Peruvian anchoveta in recycling nitrogen. Menhaden schools can modify oxygen and ammonium levels in shallow coastal water (Oviatt et al. 1972).

We thank E. Stewart for many calculations, especially those related to the pier temperature anomalies, R. Lasker and J. Hunter for editing and discussions on fish population energetics, and G. Stauffer for checking the anchovy population model. We also thank W. Thomas for editing and review. D. Gruber collected the anchovy larval data on cruises of the Food Chain Research Group. S. Tont provided discussions and introduced us to use of the pier temperature anomaly time series. We are indebted to many people for the long Scripps pier temperature and CalCOFI zooplankton and anchovy time series.

Methods

Anchovy biomass—The best description of the methods used to take the plankton net tows and estimate anchovy larval abundance is given by Kramer et al. (1972). Estimation of anchovy spawning biomass is described by Smith (1972). We derived an additional method for use here, estimation of *total* anchovy biomass from anchovy *spawning* biomass. Estimates of mortality of the central subpopulation and fecundity and proportionate maturity (MacCall 1974; Hunter and Goldberg 1980) were used to construct a stationary population. Juvenile biomass, as a proportion of total biomass, was estimated as 40% for spring, when the population biomass was at a minimum and as 68% for fall, when it was at a maximum.

Primary production—Measurements were made at 15 stations in the Southern California Bight on 15 cruises from September 1974 to July 1979. Station locations are shown elsewhere (Eppley et al. 1978). At each station water samples were taken with PVC Niskin bottles at six depths in the euphotic zone. Samples of 200-ml volume were inoculated with ^{14}C (4 μCi), incubated on deck for 24 h using neutral density screens to simulate irradiance at the sampling depths, and then filtered with Whatman GF/C glass-fiber filters. The radioactivity of the filters was measured by scintillation counting. Further details are given by Eppley et al. (1979*a*). Data were calculated as production in mg $C \cdot m^{-2} \cdot d^{-1}$ integrated over the depth of the euphotic zone.

To assess total primary production over the area of the bight, we weighted the value at each station (mg $C \cdot m^{-2} \cdot d^{-1}$) by an area of arbitrary dimensions: 85 km in the longshore direction, this being the distance between transect lines, and the geometric mean distance between stations along the transect lines. Thus the area represented by a station increased offshore because of the quasi-logarithmic distance between stations on the transect lines. The total area represented is about 30,000 km². The total production of this area was calculated as the sum of the production at each station times the area represented. Average production over the area can be expressed as the total production/total area to give t $C \cdot km^{-2} \cdot d^{-1}$ ($= g \cdot m^{-2} \cdot d^{-1}$) for each cruise.

The temperature anomaly for a given calendar date is the difference between the temperature measured on that day and the 54-year mean temperature (1920–1974) for that date. In practice this 54-year mean temperature was interpolated from mean monthly values. Daylength was interpolated for 33°N latitude from the Smithsonian Meteorological Tables.

Zooplankton—In addition to the two time series estimated for this paper—primary production 1920–1979 and anchovy spawning biomass 1951–1979—we used three previously published time series: zooplankton displacement volume (Longhurst et al. 1972); the displacement volume time series of microplankton in Santa Monica Bay (Haydock 1973); and the record of fish scale deposition rate (Soutar and Isaacs 1974) and the biomass estimates derived from them (Smith 1978). The methods used to determine plankton volume in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) are given by Ahlstrom and Thrailkill (1963) as is the derivation of $g \cdot m^{-2}$ from cm³ displacement vol · 1,000 m^{-3}.

Results

Primary production—Measured primary production ranged from 0.091 to 1.410 g $C \cdot m^{-2} \cdot d^{-1}$ during the 1974–1979 cruises. Primary production was greater nearshore than offshore, especially at stations 301–303 (Eppley et al. 1978). The maximum primary production of cruise 3 coincided with the maximum negative anomaly of Scripps pier temperatures (−2.03°C) for the week of the cruise (Fig. 2). The minimum primary production of cruise 9 coincided with the maximum positive anomaly (2.13°C). The maximum daylength for the 15-cruise series was 14.3 h and the minimum 10.1, near the total range for 33°N latitude.

For the 15-cruise series, 59% of the variation in primary production was explained by variation in Scripps pier temperature anomaly and daylength. The equation for this relationship is

$$P = \exp(-3.78 - 0.372T + 0.227D) \quad (1)$$

where P is primary production (g $C \cdot m^{-2} \cdot d^{-1}$), T is pier temperature anomaly (°C) average over the 6–8 days of each cruise, and D is daylength (h) for that period.

Values of measured primary production, estimated primary production, Scripps pier temperature anomalies, and daylength are given in Table 1 with the multiple correlation coefficients, the standard error of the coefficients, the t-test of significance of the coefficients, and the ANOVA of the regression. The statistical evaluation is based on the assumption of independence of values; serial correlation can be expected to diminish the significance levels of the coefficients moderately, but the time series is too short to examine these effects.

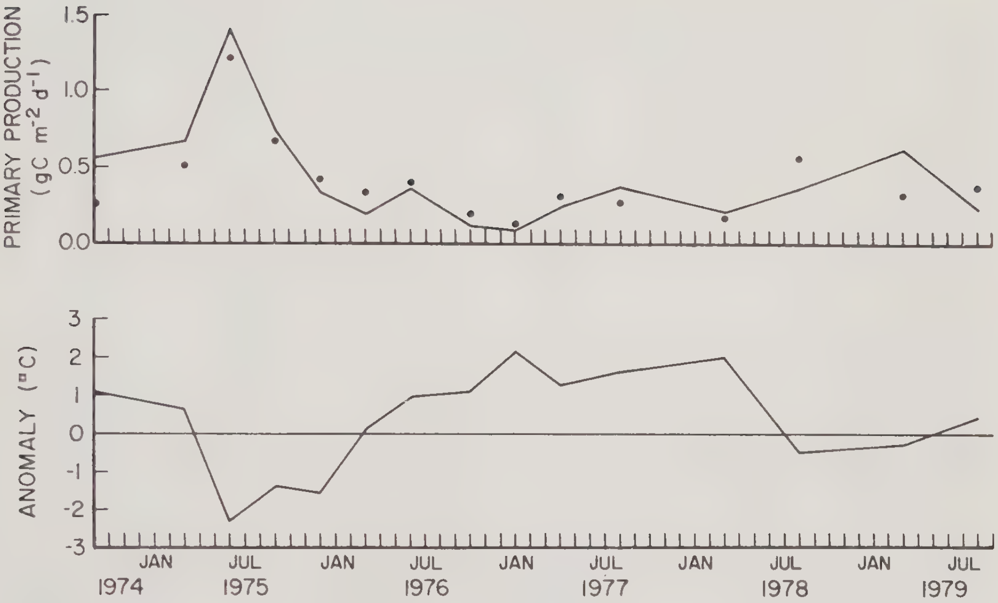

Fig. 2. Upper—time series of measured (●) and predicted (———) primary production in Southern California Bight, 1974–1979. Lower—temperature anomaly at Scripps pier during cruises.

Nonlinearity of primary production with daylength is pronounced at all temperatures. For example, in cruise 3 the average production per hour of daylength was 0.099 g $C \cdot m^{-2}$ for June, and in cruise 5 the average production per hour of daylength in December was 0.033. Overall, in warmer periods, the production per hour of daylength was 0.026 g $C \cdot m^{-2}$ in summer and 0.009 in winter. Thus daylength and the other seasonal variables it represents in Eq. 1 may account for a factor of about three in daily primary production rate at 33°N latitude.

The apparent response to the temperature anomaly is also highly nonlinear. The 15-fold variation in the temperature anomaly is associated with a factor of five in primary production. Temperature anomalies >1.2°C *below* the seasonally adjusted average were always associated with high productivity in this series. Temperature anomalies >1.5°C *above* the seasonally adjusted average were associated with lower primary production.

Estimated primary production—We used Eq. 1 with the Scripps pier temperature time series (actually the temperature anomaly) and daylength averaged for each quarter to calculate quarterly estimates and annual averages of primary production to 1920 (Table 2)—a time well before primary production could be estimated at sea. The entire time series of annual average primary production and the maximum and minimum seasonal averages are plotted in Fig. 3. The mean quarterly primary production ranged from 0.226 to 0.603 g $C \cdot m^{-2} \cdot d^{-1}$; the corresponding coefficients of variation from 25 to 31% (Table 2). The average of the annual averages is 0.392 g $C \cdot m^{-2} \cdot d^{-1}$ (SD of the annual average 0.078, C.V. 20%).

Zooplankton standing stock—The regional average of preserved zooplankton displacement volume is listed by season and year in Table 3. These values differ from those previously reported (Longhurst et al. 1972) because they are arranged in quarters centered on March, June, September, and December to correspond with the primary production time series. The months of the CalCOFI survey sampled with the highest fidelity

Table 1. Average primary production (g C·m^{-2}·d^{-1}) measurements in Southern California Bight during 15 cruises, September 1974–August 1979. Anomaly in temperature (PTA) measured at Scripps pier, averaged over the days of each cruise, is given along with mean daylength during each cruise. These parameters are used in Eq. 1 to calculate production.

	Cruise	Production	PTA (°C)	Daylength (h)	Production from Eq. 1
13–20 Sep 74	1	0.568	1.11	12.1	0.237
26 Feb–6 Mar 75	2	0.681	−1.38	11.5	0.507
16–25 Jun 75	3	1.41	−2.22	14.3	1.221
6–17 Sep 75	4	0.744	−1.40	12.5	0.664
2–10 Dec 75	5	0.336	−1.58	10.1	0.407
13–23 Mar 76	6	0.199	0.10	12.0	0.340
2–9 Jun 76	7	0.364	0.90	14.2	0.399
20–27 Oct 76	8	0.117	1.07	11.2	0.194
28 Jan–4 Feb 77	9	0.091	2.15	10.6	0.113
25 Apr–2 May 77	10	0.248	1.29	13.3	0.310
3–10 Aug 77	11	0.374	1.63	13.4	0.262
13–18 Mar 78	12	0.207	2.00	11.9	0.169
15–23 Aug 78	13	0.360	−0.48	13.1	0.577
3–8 Mar 79	14	0.638	−0.30	11.4	0.320
23–28 Aug 79	15	0.244	0.41	13.0	0.368

Eq. $P = \exp(-3.78 - 0.372T + 0.227D)$

Parameters	Coeff.	SD coeff.	Student's t
Intercept	−3.78		
PTA	−0.372	0.087	−4.23
Daylength	0.227	0.097	2.33
$r^2 = 0.65$			

ANOVA

Due to	df	SS	MS	F
Residual	12	0.56	0.05	
Regression	2	1.03	0.52	11.08
Total	14	1.59		0.002

in each season are January, April, July, and October (Eber 1977).

The seasonal cycle of average zooplankton standing stock is in phase with that of estimated primary production (Fig. 4), but has a greater range of values. This difference may only reflect the smoothing effect of the primary production equation. The mean zooplankton volumes ranged from 9.86 to 34.87 g·m^{-2}, C.V. from 42 to 73% (Table 3).

Microplankton standing crop—The Santa Monica Bay microplankton data are reported here (Table 4) primarily to point out the close relation between the weights of this mixture of net phytoplankton, detritus, and small zooplankton retained by a 0.076-mm mesh and the weight of zooplankton retained by the CalCOFI 0.55-mm silk mesh. The coefficients of variation of the annual averages are nearly identical even though the microplankton was sampled in the upper 15 m of Santa Monica Bay and the plankton displacement volume was sampled over the entire Southern California Bight from the upper 140 m of the water column. In Table 4 are listed the annual averages of primary production, microplankton, zooplankton, and northern anchovy larvae. The annual average microplankton and annual average zooplankton vary in a nonlinear way with the estimated primary production (Fig. 5). The coefficients of annual variation (Table 4) are lowest in primary production, more than twice as high in microplankton and zooplankton and more than four times as high for anchovy larvae.

Table 2. Quarterly and average annual primary production (g C·m^{-2}·d^{-1}) from Southern California Bight as estimated from primary production measurements, 1974–1979, Scripps pier temperature anomalies, and daylengths.

	Mar	Jun	Sep	Dec	Avg
1920	0.366	0.587	0.411	0.305	0.417
1921	0.451	0.489	0.471	0.229	0.410
1922	0.503	0.536	0.396	0.242	0.419
1923	0.337	0.537	0.244	0.162	0.320
1924	0.270	0.529	0.587	0.345	0.433
1925	0.367	0.449	0.398	0.144	0.340
1926	0.129	0.318	0.407	0.186	0.260
1927	0.370	0.633	0.383	0.160	0.387
1928	0.315	0.540	0.503	0.244	0.401
1929	0.460	0.424	0.276	0.165	0.331
1930	0.250	0.559	0.315	0.132	0.314
1931	0.142	0.227	0.219	0.254	0.211
1932	0.383	0.616	0.556	0.278	0.458
1933	0.485	0.922	0.673	0.299	0.595
1934	0.230	0.367	0.334	0.178	0.277
1935	0.409	0.488	0.407	0.251	0.389
1936	0.334	0.384	0.239	0.178	0.284
1937	0.412	0.424	0.332	0.168	0.334
1938	0.329	0.692	0.368	0.272	0.415
1939	0.501	0.533	0.291	0.100	0.356
1940	0.238	0.576	0.352	0.157	0.331
1941	0.168	0.526	0.384	0.164	0.311
1942	0.352	0.536	0.351	0.200	0.360
1943	0.293	0.685	0.335	0.186	0.375
1944	0.347	0.796	0.454	0.215	0.453
1945	0.489	0.617	0.285	0.299	0.423
1946	0.397	0.421	0.346	0.264	0.357
1947	0.314	0.490	0.357	0.268	0.357
1948	0.463	0.781	0.473	0.340	0.514
1949	0.515	0.837	0.352	0.294	0.500
1950	0.399	0.681	0.450	0.235	0.441
1951	0.356	0.553	0.490	0.215	0.404
1952	0.403	0.774	0.456	0.251	0.471
1953	0.458	0.710	0.481	0.244	0.473
1954	0.359	0.502	0.413	0.229	0.376
1955	0.457	0.656	0.315	0.317	0.436
1956	0.482	0.685	0.362	0.204	0.433
1957	0.315	0.456	0.336	0.130	0.309
1958	0.193	0.587	0.278	0.115	0.293
1959	0.193	0.304	0.233	0.154	0.221
1960	0.334	0.656	0.456	0.216	0.416
1961	0.304	0.680	0.479	0.301	0.441
1962	0.407	0.911	0.429	0.230	0.494
1963	0.338	0.652	0.323	0.159	0.368
1964	0.339	0.920	0.356	0.352	0.492
1965	0.348	0.890	0.392	0.194	0.456
1966	0.339	0.527	0.324	0.218	0.352
1967	0.357	0.773	0.252	0.195	0.394
1968	0.357	0.595	0.377	0.230	0.365
1969	0.377	0.704	0.445	0.207	0.433
1970	0.326	0.719	0.394	0.253	0.423
1971	0.537	0.595	0.332	0.418	0.471
1972	0.409	0.484	0.338	0.168	0.350
1973	0.309	0.677	0.525	0.326	0.459
1974	0.439	0.634	0.326	0.300	0.425
1975	0.530	0.893	0.671	0.342	0.609
1976	0.389	0.493	0.338	0.095	0.329
1977	0.290	0.678	0.362	0.126	0.364
1978	0.199	0.612	0.304	0.229	0.336
1979	0.346	0.657	0.293	0.222	0.380
Mean	0.357	0.603	0.384	0.226	0.392
SD	0.097	0.155	0.097	0.070	0.078
C.V. %	27	26	25	31	20

Northern anchovy spawning biomass—The time series of abundance of anchovy larvae are listed in Table 4 (annual values) and Table 5 (quarterly values). These values are a subset of those reported for the California Current (Smith 1972; Stauffer and Parker: SW Fish. Center Admin. Rep. LJ-78-9; Stauffer: SW Fish. Center Admin. Rep. LJ-79-22). They were assessed every third year after 1966.

The seasonal abundance of anchovy larvae is out of phase with primary production and zooplankton volume. Anchovy larvae show a seasonal maximum in January–March, while primary production and zooplankton biomass maxima are centered on June (*see quarterly mean values:* Tables 2, 3, 5). This phase difference has been noted before for anchovy

Table 3. Zooplankton standing stock (g·m^{-2}).

	Mar	Jun	Sep	Dec	Avg
1951	15.22	21.16	7.00	8.52	12.98
1952	12.63	20.40	17.50	10.50	15.26
1953	16.59	66.51	31.05	6.54	30.18
1954	10.96	32.12	9.13	7.61	14.95
1955	11.26	24.51	13.09	13.39	15.56
1956	17.35	42.31	22.83	22.69	26.29
1957	16.59	14.16	5.63	4.57	10.24
1958	7.00	11.26	2.44	2.28	5.75
1959	5.02	8.52	7.30	5.78	6.66
1960	13.09	20.09	9.74	3.65	11.64
1961	14.61	44.60	6.85	9.89	18.99
1962	26.03	100.76	24.20	8.07	39.76
1963	21.46	71.99	7.31	15.68	29.11
1964	28.77	37.14	42.01	15.37	30.82
1965	10.05	20.09	17.50	7.46	13.77
1966	14.00	22.22	20.55	15.81	18.15
Mean	15.04	34.87	15.26	9.86	18.76
SD	6.28	25.40	10.80	5.44	9.71
C.V. %	42	73	71	55	52

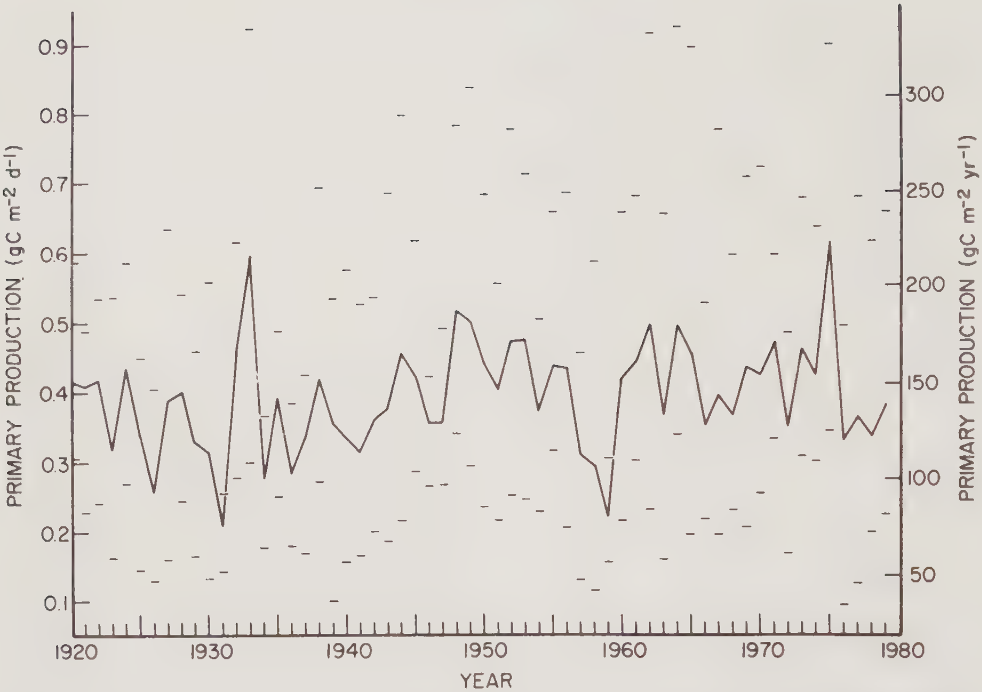

Fig. 3. Estimated annual primary production in Southern California Bight, 1920–1979. Dashes indicate maximum and minimum seasonal production rates for each year. Data from Table 2 indicate that maximum seasonal production is in June quarter in 93% of the years and that minimum seasonal production is in December quarter 85% of the years.

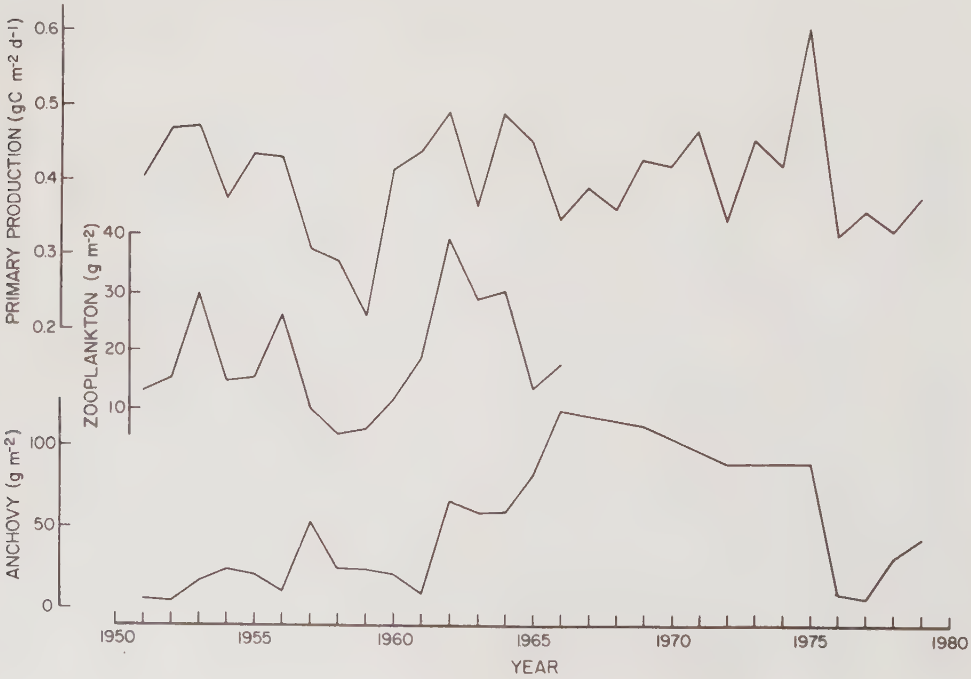

Table 4. Annual average primary production (g $C \cdot m^{-2} \cdot d^{-1}$), microplankton and zooplankton standing stock ($g \cdot m^{-2}$), and anchovy larvae ($No. \cdot m^{-2}$).

	Primary productivity	Micro-plankton*	Zooplankton	Larval northern anchovy
1951	0.404	29	13	5.1
1952	0.471	35	15	3.9
1953	0.473	78	30	14.6
1954	0.376	39	15	21.9
1955	0.436	37	16	18.8
1956	0.433	78	26	9.2
1957	0.309	31	10	48.7
1958	0.293	18	6	22.8
1959	0.221	18	7	21.4
1960	0.416	28	12	19.7
1961	0.441	43	19	9.0
1962	0.494	98	40	59.0
1963	0.368	67	29	53.7
1964	0.492	76	31	55.7
1965	0.456	39	14	(77.4)†
1966	0.352	41	18	116.1
Mean	0.402	47.2	18.8	34.8
SD	0.078	24.2	9.7	31.1
C.V. %	19	51	52	89

* Santa Monica Bay, upper 15 m only.

† Estimated from samples in winter, spring, and summer quarters only.

eggs and plankton volume (Smith and Lasker 1978). The mean abundance of anchovy larvae in winter (January, February, and March) is $74.2 \cdot m^{-2}$ (SD 74.9, C.V. 101%) for the 19-year series. The mean abundance in spring is $66.0 \cdot m^{-2}$ (SD 63.7, C.V. 97%). The mean autumn abundance is $7.7 \cdot m^{-2}$ (SD 10.6, C.V. 138%). The mean of annual seasonal averages is $43.9 \cdot m^{-2}$ (SD 36.1, C.V. 82%). Most of the coefficient of variation is due to the extreme trend in abundance. The means comparable to the primary production and zooplankton standing stock seasons are "March" 71.5, "June" 50.1, "September" 14.8, and "December" 29.9 larvae$\cdot m^{-2}$.

An apparent relationship of anchovy larvae to zooplankton abundance and phytoplankton production—Although the annual values in Fig. 4 suggest no dependence of anchovy larvae on plankton, statistical exploration of the quarterly values has led us to postulate a relationship between the abundance of anchovy larvae and the zooplankton standing stock and primary production in the study area. The 59 quarterly production values (Table 2), zooplankton standing stocks (Table 3), and the northern anchovy larvae from 1951–1965 (Table 5) are all positively intercorrelated to a moderate degree. In addition to the direct correlation, the zooplankton-anchovy larvae cross-correlation was maximum at a lag of three

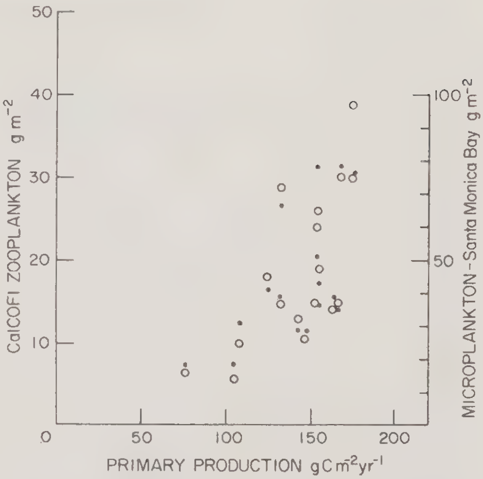

Fig. 5. Comparison of zooplankton concentrations in Southern California Bight with estimated primary production in the bight. Zooplankton data are from two series. ○—From bight portion of CalCOFI station grid which covers California Current region. ●—Data from Santa Monica Bay collected by personnel of the City of Los Angeles Hyperion Waste Treatment facility. Values are annual averages of monthly (CalCOFI) or weekly (Hyperion) net collections. Mesh of CalCOFI nets was 0.505 mm, that of Hyperion net was finer (about 0.076 mm). For comparing these values on the same scale one can use an exponential curve of the form $z = a \exp(bP)$ where a is intercept, b is slope, z is zooplankton average annual concentration in $g \cdot m^{-2}$, and P is primary production in g $C \cdot m^{-2} \cdot yr^{-1}$. For Southern California Bight zooplankton with the CalCOFI net, constant a is 1.97 and b is 0.014. For Santa Monica Bay microplankton, a is 6.25 and b is 0.013.

←

Fig. 4. Estimated annual primary production, annual mean CalCOFI zooplankton concentrations, and anchovy total biomass in Southern California Bight.

Table 5. Time series of abundance of northern anchovy larvae (No.·m^{-2}) in Southern California Bight study area.

	Feb	May	Aug	Nov	Avg
1951	2.5	9.6	1.9	6.4	5.1
1952	1.7	5.6	5.5	2.8	3.9
1953	9.1	4.1	10.9	34.2	14.6
1954	64.0	12.7	9.5	1.3	21.9
1955	30.9	19.3	23.5	1.3	18.8
1956	4.9	19.5	10.1	2.1	9.2
1957	104.9	77.5	10.3	2.0	48.7
1958	36.1	48.1	6.3	0.5	22.8
1959	31.7	52.3	0.9	0.7	21.4
1960	41.3	32.7	4.4	0.4	19.7
1961	1.5	26.2	7.9	0.3	9.0
1962	51.2	154.4	28.4	2.0	59.0
1963	150.3	60.9	1.1	2.3	53.7
1964	87.5	117.7	4.6	12.8	55.7
1965	136.3	116.7	43.6	22.1	98.9 (77.4)
1966	167.0	221.4	53.9	12.2	116.1
1969	259.3	83.6	42.7	—	99.5
1972	36.6	175.4	55.7	27.4	89.2 (70.0)
1975	193.9	16.8	28.9	—	66.8
N	19	19	19	17	19
Mean	74.2	66.0	18.4	7.7	43.9
SD	74.9	63.7	18.4	10.6	36.1
C.V. %	101	97	100	138	82

Table 6. Prediction of quarterly achovy larvae in Southern California Bight area from zooplankton standing stock and phytoplankton production.

	Anchovy larvae (*A*)	Lagged zooplankton (*Z*)	Primary production (*P*)
Anchovy larvae (*A*)			0.41
Lagged zoolpankton (*Z*)		0.54	−0.04

Regression Eq.: $A = 298 + 12.58Z + 904P$

Parameters	Coeff.	SD coeff.	Student's *t*
Intercept	−298	104	−2.88
Z	12.58	2.24	5.61
P	904	206	4.39

$r^2 = 46.0\%$ adjusted for df

Due to	df	ANOVA SS	MS	*F*
Residual	53	4,786,028	90,302	
Regression	2	4,404,895	2,202,448	24.39
Total	55	9,190,923		

quarters for the anchovy. The multiple correlation parameters of the abundance of anchovy larvae as determined by the zooplankton standing stock three quarters previously and the primary production of the same quarter are summarized in Table 6. The relationship explains only 46% of the abundance of larvae, but the *t*-ratio is highly significant for both zooplankton and primary production. The ANOVA of the regression *F*-test is also highly significant. These relationships would suggest that the intensity of spawning activity of the adult anchovy in part depends on zooplankton abundance three quarters earlier and in part on the productivity of the area in the same season. This might be expected if the fish accreted fat (Smith and Lasker 1978) in the preceding year which enhanced subsequent reproduction.

Adult and juvenile anchovy biomass—The estimated spawning biomass of anchovy is derived from the "larval index" (Smith 1972; Smith and Burris: SW Fish. Center Admin. Rep. LJ-78-24; Stauffer and Parker: SW Fish. Center Admin. Rep. LJ-78-9), which is used for management of the U.S.-based fishery. The time series of estimated spawning biomass (Table 7) illustrates the nature of the annual variability of biomass density of the Southern California Bight portion of the subpopulation habitat. The local density in g·m^{-2} increased 12-fold in the 5 years 1952–1957, decreased 5-fold in the 4 years 1957–1961, and increased 12-fold in the 5 years 1961–1966. The maximum annual increase was 6-fold in 1961–1962 and the maximum annual decrease was 8-fold in 1975–1976. The total range of values was 28-fold. Since the study area does not contain the entire population, these changes may involve both reproduction and migration. Sampling error, particularly at higher population densities, is of course appreciable, and both bias and imprecision may be contributing to extreme values. In Fig. 6 the Southern California Bight time series is plotted with the time series of the entire central subpopulation. The population increases of 1957 and 1962, for example, were not

Table 7. Anchovy juvenile and adult biomass and Southern California Bight biomass density.

Year*	Spawning biomass estimated			Total biomass assumed		Autumn biomass assumed	
	g	$g \cdot m^{-2}$	% of central subpop.	g	$g \cdot m^{-2}$	g	$g \cdot m^{-2}$
1951	5.4×10^{10}	1.80	34	9.1×10^{10}	3.03	1.7×10^{11}	5.67
1952	4.2	1.40	30	7.1	2.37	1.3	4.33
1953	1.6×10^{11}	5.33	35	2.7×10^{11}	9.00	5.0	16.67
1954	2.3	7.67	33	3.9	13.00	7.2	24.00
1955	2.0	6.67	26	3.4	11.33	6.2	20.67
1956	9.8×10^{10}	3.27	22	1.6	5.33	3.0	10.00
1957	5.2×10^{11}	17.33	47	8.7	29.00	1.6×10^{12}	53.33
1958	2.4	8.00	19	4.0	13.33	7.5×10^{11}	25.00
1959	2.3	7.67	16	3.9	13.00	7.2	24.00
1960	2.1	7.00	15	3.5	11.67	6.5	21.67
1961	1.0	3.33	9	1.7	5.67	3.0	10.00
1962	6.3	21.00	23	1.1×10^{12}	36.67	2.0×10^{12}	66.67
1963	5.7	19.00	15	1.0	33.33	1.8	60.00
1964	5.9	19.67	23	1.0	33.33	1.8	60.00
1965	7.9	26.33	19	1.3	43.33	2.5	83.33
1966	1.2×10^{12}	40.00	38	2.0	66.67	3.7	123.33
1969	1.1×10^{12}	36.67	41	1.8	60.00	3.4	113.33
1972	7.1×10^{11}	23.67	28	1.2	40.00	2.2	73.33
1975	7.1×10^{11}	23.67	22	1.2	40.00	2.2	73.33
1976	8.9×10^{10}	2.97	—	1.5×10^{11}	5.00	2.8×10^{11}	9.33
1977	6.2×10^{10}	2.07	—	1.0	3.33	1.9	6.33
1978	3.0×10^{11}	10.00	25	5.0	16.67	9.4	31.33
1979	4.0×10^{11}	13.33	25	6.7	22.23	1.3×10^{12}	43.33
N		23			23		23
Mean		13.38			22.49		41.69
SD		11.18			18.64		34.67

* No data for 1967, 1968, 1970, 1971, 1973, or 1974.

confined to the study area but in fact extended offshore more than 370 km (Smith 1972: fig. 11; Kramer and Ahlstrom 1968).

Comparison of the annual time series of phytoplankton production, zooplankton standing stock, and the assumed annual maximum biomass of anchovy (Fig. 4) shows coincidental local minima of almost 3 years' extent in the late 1950s during a North Pacific equivalent of the Peruvian "El Niño." Concurrent increases in total anchovy population (Fig. 6) suggest, however, that this decrease in anchovy was essentially a local or coastal phenomenon confined to the Southern California Bight.

Energetics—After 1957, the total subpopulation of northern anchovy increased in the succeeding years but the Southern California Bight portion of the population decreased (Fig. 6). In 1966, the local portion of the population reached a maximum in the time series. The years 1957 and 1966 are interesting ones for examining the energy requirements of anchovy in relation to zooplankton and primary production, as these years were anchovy biomass maxima in the bight. We will examine anchovy egg production as one aspect of limiting energetics. Respiration and growth cannot be usefully estimated because the distribution of swimming speed and of age composition is not known, but if we use the reproductive rate calculated for the current population (Hunter and Goldberg 1980; Hunter pers. comm.), the rate of egg production can be estimated. The spawning biomass in 1957 was 17.33 $g \cdot m^{-2}$ or 8.67 $g \cdot m^{-2}$ of females. Egg production is now estimated at $389 \cdot g^{-1}$ of female per batch for 20 batches (Hunter pers. comm.). The calorific value of a $3.01 \times 10^{-5} \cdot g^{-1}$ anchovy egg is $1.64 \times$

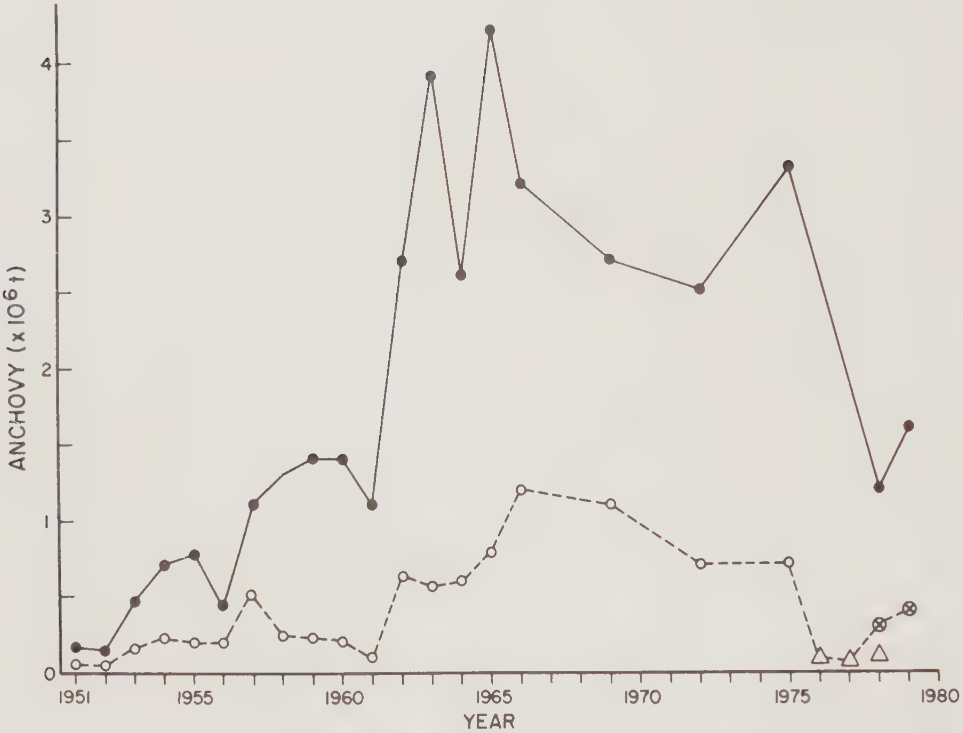

Fig. 6. Estimated spawning biomass of central subpopulation of northern anchovy (Stauffer: SW Fish. Center Admin. Rep. LJ-79-22, ●) and that segment spawning in Southern California Bight study areas (Smith and Burris: SW Fish. Center Admin. Rep. LJ-78-24, ○). The 1976–1978 figures (△) were obtained by ratio of Southern California Bight studies anchovy larvae to those of CalCOFI winter cruises of 1975. The 1978–1979 figures (⊗) were obtained by a fixed ratio (0.25) of central subpopulation. No estimates of central subpopulation spawning biomass are available for 1967–1968, 1970–1971, 1973–1974, and 1976–1977.

10^{-4} kcal (Hunter pers. comm.). Egg production is then 11 kcal·m^{-2}·yr^{-1}. In 1957 primary production was 113 g C·m^{-2}. If the calorific value is 11.4 kcal·g^{-1} C (Platt and Irwin 1973), then the reproduction investment in eggs of anchovy was about 0.9% of the annual primary production. (In the ensuing 4 years, the spawning biomass decreased by a factor of five.)

In 1966 the values were: Phytoplankton production = 1,466 kcal·m^{-2}·yr^{-1}, maximum anchovy biomass = 173 kcal·m^{-2}, anchovy spawning biomass = 56 kcal·m^{-2}, and egg production = 26 kcal·m^{-2}. The egg production in 1966 was then apparently 1.8% of the local phytoplankton production. If anchovy reproduction is about 10% of ration (Hunter and Leong pers. comm.) then that ration was about 18% of primary production in 1966.

Long term population changes—Soutar and Isaacs (1974) used fish-scale deposition rates as recorded in the varved sediments of the Santa Barbara Basin to estimate relative anchovy abundance for the period 1785–1970 in 5-year intervals. Recent estimates of absolute population biomass were used (Smith 1978) to assign values to the anchovy and other populations detected by scale deposition. No significant correlations with primary production were found for the anchovy biomass, the total *epipelagic* biomass which includes Pacific sardine (*Sardinops sagax caerulea*), the Pacific mackerel

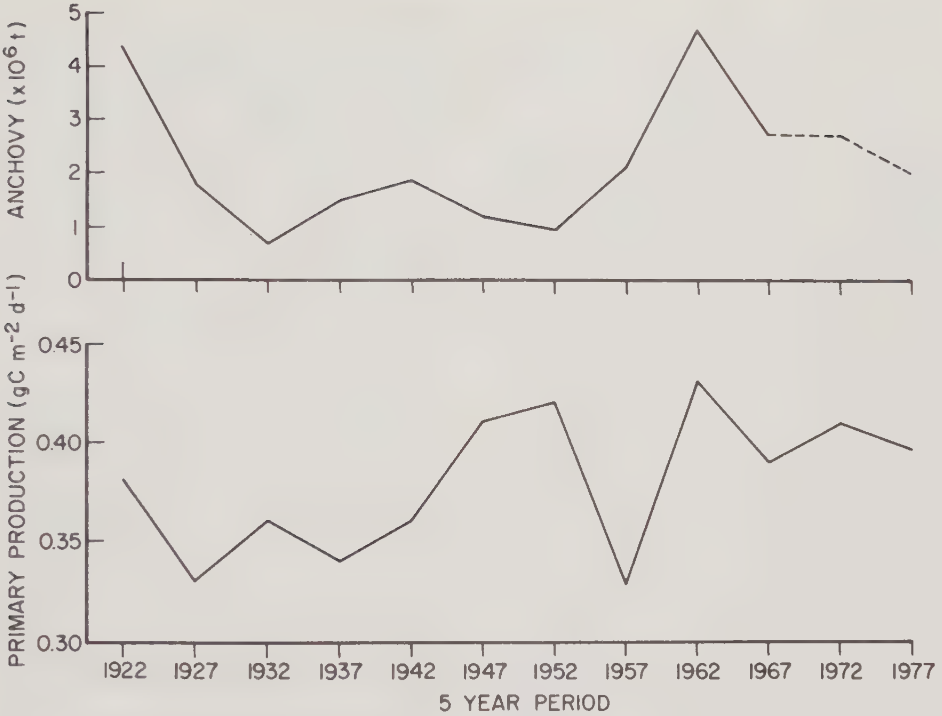

Fig. 7. Five-year mean values for anchovy biomass and estimated primary production, 1920–1979.

(*Scomber japonicus*), and the Pacific saury (*Cololabis saira*), or the total pelagic biomass which includes also the Pacific hake (or whiting, *Merluccius productus*). The maximum correlation coefficient was only 0.3 for the northern anchovy (Fig. 7).

Discussion

The primary production time series—The temperature anomaly–daylength model includes two variables that control phytoplankton production: the rate of nutrient input and the seasonal change in photosynthesis. Departures from historical mean temperatures (the temperature anomalies) were correlated with phytoplankton standing stock as reflected by particulate organic nitrogen concentrations (mg $PON \cdot m^{-2}$) and with the depth of the nitrate concentration gradient (Eppley et al. 1978). It was later shown that the depth of the nitrate concentration gradient is related to the rate of nitrate uptake by phytoplankton in the euphotic zone and to the rate of primary production (Eppley et al. 1979*a*). The position of the nitracline evidently reflects the rate of nitrate input to the euphotic zone. Seasonal changes in photosynthetic rate per weight of chlorophyll, i.e. the productivity index, were also apparent (Eppley et al. 1977). Daylength is an appropriate variable to represent the suite of environmental factors that alter photosynthetic rate with season (such as irradiance and temperature), and it is independent of the temperature anomaly.

The temperature anomaly becomes coherent at different locations within the bight for periods longer than about 4–5 days (List and Koh 1976). The average anomaly over the 6–8-day cruise periods, as used here, is considered representative of events taking place throughout the bight. These events include coastal upwelling, advection associated, for example, with current flows, and interannual differences in ocean climate.

The station grid (Eppley et al. 1978) or any other fixed station pattern, cannot be expected to provide synoptic data. Nor can the Scripps pier temperature be expected to reflect all events that influence the depths of the nitrate concentration gradient throughout the bight. That primary production (based on the Scripps pier temperature anomalies) was correlated with microplankton in Santa Monica Bay suggests, however, that the estimated primary production may be representative over 150 km along the coast. Satellite images of both temperature (R. Lasker pers. comm.) and chlorophyll (R. C. Smith pers. comm.) show different values in the Southern California Bight from those in the California Current regime some 150–200 km offshore. The images also suggest that the station pattern is representative within the bight, except for the Santa Barbara Basin in the extreme northwest portion well north of the station grid. These observations and the correlations between primary production and zooplankton suggest that we have made progress toward assessing the carrying capacity of the region for herbivores.

The estimating algorithm also promises to be useful with respect to contemporary events in the bight. For example, we are using it as a first-line "verification" of production estimated from chlorophyll data derived from the satellite images. In this role it serves as a first-order estimate when no cruise measurements are available, i.e. on all but infrequent occasions.

We anticipate that this simple approach to estimating primary production may prove useful in other subtropical and tropical areas. Tont (1976) found that diatom outbursts occurred historically off the Scripps pier during short period fluctuations in the pier temperature anomaly. Diatoms were associated with cold anomalies, i.e. upwelling. Three major blooms account, on average, for 85% of the annual diatom biomass at the pier. Herbland and Voituriez (1979) found an even stronger correlation between primary production and the depth of the nitracline in parts of the eastern tropical Atlantic than we found here. Nevertheless it is not clear why the Scripps pier temperature anomaly is so well correlated with the depth of the nitracline in the bight, as the surface waters are stratified except during strong upwelling events and the nitracline lies at a mean depth of 16 m on the shelf and deeper offshore. Further, the nitracline shows vertical displacements in response to the semidiurnal internal tides of as much as 15 m over 24 h (Eppley et al. unpubl.). Although it would not be surprising if other variables and other time scales (Tont 1976) ultimately prove more useful in estimating production than the temperature anomaly, it is surprising to us that the pier temperature anomaly and daylength account for as much of the variability in production as they do. For cruises 2–13, for example, the r^2 for the correlation between measured and predicted production is >0.8.

Two new time series pertinent to plankton and fisheries have been prepared from CalCOFI hydrographic data (about 1950–present). Chelton (1980) has developed a "California El Niño" index of low frequency changes in steric height (from hydrography) observations in the California Current region. Bernal (1980) developed a time series index of anomalies in the strength of California Current flow based on the southward extension of its low salinity core. Both indices are correlated with zooplankton concentrations in the California Current, as is estimated primary production.

Time scales—On the geologic time scale it is clear that the seasonal upwelling and equatorward transport of the eastern boundary currents foster and maintain major populations of pelagic schooling fishes in several areas of the world (Cusing 1969). It is also quite clear from our study that increasing daylength in the bight each spring stimulates primary production, secondary production, and the production of spawn in the dominant fish population. With the exception of the sustained decrease of primary production in the warm water years of 1958–1959, and the coincident decrease in the anchovy biomass in the bight (Figs. 4, 6, 7), there is little evidence for annual or 5-year-time-scale control of anchovy abundance by primary production.

Nutrient regeneration—The concepts of new vs. regenerated primary production have not yet entered into the discussion of transfer efficiency in the literature. New production was defined by Dugdale and Goering (1967) as that resulting from allochthonous nutrient entering the euphotic zone. In local waters this is primarily nitrate from subeuphotic waters (Eppley et al. 1979*a*). Elsewhere river water, rain, or nitrogen fixation might be important nutrient sources for new production. Regenerated production results from nutrient recycling within the euphotic zone. In Southern California Bight waters new production averaged about 35% and regenerated production 65% of total production. New production can be viewed as that fraction of primary production available for export from the euphotic zone, i.e. the amount that can be removed without a decline in phytoplankton production, as long as the nutrient input rate remains unchanged. Most of the export is the sinking flux of particulate organic matter, such as in fecal pellets. The fish catch accounts for only a small fraction of global new production (Eppley and Petersen 1979).

Both zooplankton and anchovies are important in nutrient recycling in the bight (McCarthy and Whitledge 1972). The anchovy is a schooling fish and this behavior must contribute to patchiness of regenerated nutrients such as ammonium. Oviatt et al. (1972) found elevated ammonium concentrations behind menhaden schools in the coastal Atlantic. Our rough calculations suggest that the average ambient ammonium concentration of 0.35 μM (Eppley et al. 1979*b*) should be approximately doubled behind an anchovy school. If we assume an anchovy concentration of 15×10^3 g wet wt$\cdot$m^{-2} within a school (Hewitt et al. 1976) and 0.28 dry wt:wet wt we get a school biomass 4.2×10^3 g dry wt$\cdot$m^{-2}. If the ammonium excretion rate is 0.1×10^{-3} mol N$\cdot$(g dry wt)$^{-1}\cdot$d^{-1} (for other rates *see* McCarthy and Whitledge 1972), the daily nitrogen excretion is 0.4 mol N$\cdot$m^{-2}. Further, if the thickness of the school is 10 m and the school occupies a water mass for 10 min, the ammonium input will be 0.3×10^{-3} mol N$\cdot$m^{-3} in 10 min. For comparison, the mean ammonium assimilation rate by phytoplankton in the bight is about 0.13×10^{-3} mol N$\cdot$m$^{-3}\cdot$d^{-1}, which could be supplied by a fish school in 5 min. McCarthy and Kamykowski (1972) found elevated levels of urea-N in La Jolla Bay for several weeks associated with a high incidence of blue sharks, another example of the importance of fish in pelagic nutrient recycling.

Concentration of schooling fish—The anchovy schooling behavior may be significant in providing nutrients for phytoplankton in two different ways, as it imposes both spatial and temporal variability in nutrient distribution. The temporal variability in nutrient input rate could influence relative phytoplankton species success, as demonstrated in cultures by Turpin and Harrison (1980). The spatial variability is characterized by brief but intense local episodes of grazing and nutrient excretion. Conversely, the long intervals between these episodes promotes local recovery of prey in an environment enriched by the excreted nutrients.

In the absence of predation on the phytoplankton and the nutrient recycling associated with it, new production would be equivalent to total production, as in an axenic algal culture. Nutrient recycling increases total production by 2-fold, on an average, in the Southern California Bight (Eppley et al. 1979*a*). The closest approach to a total absence of epipelagic fish in the bight was during the hiatus after the decline of the sardine and before the rise of the anchovy in the late 1950s (Smith 1978). Such biological interaction as nutrient regeneration by fish would not be evident in the estimated annual primary production because the latter is calculated from the physical variables. However, the zooplankton and microplankton time series might reflect the role of fish in nutrient recycling. Clearly fish predation is not a major regulator of zooplankton stocks since primary production and zooplankton are correlated (Fig. 5). However, ratios of zooplankton biomass to estimated primary production might be revealing with respect to nutrient recycling via fish. Average ratios (from Table 4) are 0.035 for 1951–1960 when anchovy biomass was low and 0.050 for 1961–1966 when it was higher, suggesting that there was a larger zooplankton biomass per unit primary production when anchovies were abundant than when they were less abundant. In other words if a constant ratio exists between zooplankton and primary production, production may be underestimated because of failure to include nutrient regeneration by fish in the estimating algorithm.

Transfer efficiencies—The anchovy egg production in the bight was apparently as much as 1.8% of primary production in 1966, the year of maximum anchovy biomass. We have also estimated that anchovy food consumption was about 18% of the primary production in 1966. These values suggest rather high anchovy predation on zooplankton in 1966, but no crash of the zooplankton biomass is apparent in Fig. 4. Steele and Frost (1977) suggested that fish predation might be very dependent on the size of individual zooplankton. Koslow (1980) showed that the predation of anchovy schools on zooplankton off southern California was size-dependent, with larger animals taken in preference to small, depending somewhat on the size distribution of zooplankton encountered by the school. The CalCOFI zooplankton collections have not yet been analyzed from the standpoint of differentiating different size groups or taxa in the plankton. Cushing (1975) reviewed information on the transfer efficiency of the herbivore trophic level; values of about 0.2 are common, which are supported by our calculations of about 0.18.

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CURRENT UNDERSTANDING OF THE STATUS OF SMALL CETACEAN POPULATIONS IN THE BLACK SEA

T.D. Smith

Abstract

A fishery using guns and nets for the common dolphin, *Delphinus delphis*, Azov dolphin, *Phocoena phocoena*, and bottlenose dolphin, *Tursiops truncatus*, in the Black and Azov Seas has been pursued since about 1870 from the USSR, Turkey, Bulgaria and Romania. Steadily declining annual Soviet harvests since the maximum Soviet catch of 135 000-140 000 animals in 1938, despite an increased catching effort, led to seasonal management restrictions by the USSR in 1962, and a complete closure of the fishery in the USSR, Romania and Bulgaria in 1967. The final annual Soviet catches of 5 600-7 400 animals reported for 1964-66 represent a major collapse of the fishery and were accompanied by apparent marked changes in the age and sex composition of the harvest and a change in the species composition from the historically predominant *D. delphis* to predominantly *P. phocoena*. The fishery continues in Turkey with recent reported annual catches approaching the 1938 Soviet maximum; the loss rate is estimated to be high because of the use of guns as the harvesting method.

Limited catch statistics are available since 1927, except for Romania, and are generally reported only for all species combined in total metric weight. Analysis indicates that the exploitation rate was probably excessive at the height of the fishery in 1936 (12.5-20.0 %) and may remain so today for the Turkish fishery (7.9-100.8 %).

Annual Soviet aerial surveys initiated since the 1967 moratorium provide questionable estimates of total population size of Black Sea porpoises. Problems with these estimates and probably also with kill estimates preclude definite understanding of the present state of the population and indicate the need to refine both these statistics. Present observations are confined to recognition that the numbers of porpoise in the Black Sea have declined substantially to marginal levels due to the direct fishery; the present Turkish fishery is important, particularly as it continues now when stocks are probably reduced.

Résumé

Le dauphin commun, *Delphinus delphis*, le “dauphin” de la mer d’Azov, *Phocoena phocoena*, et le souffleur, *Tursiops truncatus*, sont pêchés aux armes à feu et au filet depuis 1870 environ dans la mer Noire et la mer d’Azov par l’URSS, la Turquie, la Bulgarie et la Roumanie. La diminution régulière des captures de l’URSS depuis le maximum soviétique de 135 000-140 000 animaux en 1938, malgré un effort de capture accru, a amené ce pays à adopter des restrictions saisonnières en 1962. La pêche a été entièrement arrêtée par l’URSS, la Roumanie et la Bulgarie en 1967. Le chiffre annuel des dernières captures soviétiques en 1964-66, 5 600-7 400 animaux, représente un effondrement majeur de la pêche, qui s’est accompagné de changements nettement marqués de la composition des captures par âge et par sexe. La composition par espèce était également modifiée, *D. delphis*, qui avait toujours été l’espèce dominante, cédant la place à *P. phocoena*. La pêche se poursuit en Turquie; les

captures annuelles récentes signalées avoisineraient le record soviétique de 1938. On estime que le taux de perte est élevé par suite de l'emploi des armes à feu comme méthode d'exploitation.

On possède des statistiques de capture limitées depuis 1927, sauf pour la Roumanie. Elles donnent en général le poids total pour l'ensemble des espèces. L'analyse indique que le taux d'exploitation a été probablement excessif lors de l'apogée de la pêche en 1936 (12,5-20 %) et qu'il peut l'être encore dans la pêcherie turque (7,9-100,8 %).

Les enquêtes aériennes annuelles entreprises par les Soviétiques depuis le moratoire de 1967 fournissent des estimations d'une fiabilité contestable sur la taille totale des populations de marsouins de la mer Noire. L'incertitude de ces estimations et probablement aussi des estimations de la mortalité par pêche ne permet pas de connaître exactement l'état actuel de la population et prouve qu'il est nécessaire d'améliorer ces deux types de statistiques. A l'heure actuelle, on doit se borner à reconnaître que les effectifs des marsouins de la mer Noire ont subi un fléchissement substantiel et sont tombés à un niveau marginal du fait de la pêche directe. La pêche turque actuelle est d'autant plus importante qu'elle se poursuit à un moment où les stocks sont probablement réduits.

Extracto

Desde 1870, aproximadamente, la URSS, Turquía, Bulgaria y Rumania se dedican a la pesca de delfín común, *Delphinus delphis*, marsopa de Azov, *Phocoena phocoena*, y tursión, *Tursiops truncatus*, con redes y armas de fuego, en el mar Negro y el mar de Azov. La continua disminución de las capturas anuales de la Unión Soviética (a pesar del aumento del esfuerzo de captura) respecto a la cifra máxima de 135 000-140 000 animales conseguida en 1938 movió a ese país a introducir en 1962 restricciones, regulando la temporada de caza. En 1967, la URSS, Rumania y Bulgaria vedaron totalmente la captura de esos animales. Las últimas capturas anuales de la Unión Soviética (5 600-7 400 animales), correspondientes a 1964-66, reflejan el gran colapso de esa actividad y revelan notables cambios en la composición por edad y sexo de los animales capturados y en la composición por especies de las capturas, con un predominio de *P. phocoena* frente al predominio tradicional de *D. delphis*. En Turquía prosigue la explotación de esos delfínidos, con capturas que, en los últimos años, según los datos comunicados, se acercan a las cifras máximas de la Unión Soviética de 1938. Se calcula que el índice de pérdidas es elevado debido al empleo de armas de fuego.

Se dispone de estadísticas limitadas de captura desde 1927 (con exclusión de Rumania), que en general se refieren sólo al conjunto de todas las especies, indicando el peso total en unidades métricas. Los análisis realizados indican que probablemente el índice de explotación en el momento culminante de la pesquería (1936) era excesivo (12,5-20 por ciento) y tal vez siga siéndolo hoy día en Turquía (7,9-100,8 por ciento).

Los reconocimientos aéreos realizados anualmente por la Unión Soviética desde la veda de 1967 permiten hacer estimaciones, de valor cuestionable, sobre el volumen total de la población de delfines y marsopas del mar Negro; los problemas inherentes a esas estimaciones y, probablemente también, a las estimaciones de las capturas impiden conocer claramente la situación actual de las poblaciones y ponen de relieve la necesidad de mejorar ambas estadísticas. En la actualidad, lo único que se puede hacer es reconocer que el número de delfines y marsopas del mar Negro ha disminuido sustancialmente, como consecuencia de la explotación, reduciéndose a cifras marginales. Las actuales actividades pesqueras de Turquía son importantes, sobre todo porque probablemente las poblaciones han disminuido.

T.D. Smith
Southwest Fisheries Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, California 92038, USA

Introduction

In 1962, the USSR adopted unilateral management restrictions on whaling in the international multispecies small cetacean fishery in the Black and Azov Seas, which took the form of a restriction on killing during the breeding season. In 1967, whaling by the USSR, Romania and Bulgaria was completely stopped. In Turkey whaling continues. The adoption of management restrictions by the other nations was prompted by steadily declining catches since 1939, and the catastrophic decline in catch in 1964-66.

The information available to me on this fishery comes from: Danilevsky and Tuyutyunnikov, 1968; Zemsky and Yablokov, 1974; Mitchell, in press – draft version; personal communication with Zemsky and Yablokov, December 1964, in La Jolla, California.

There are several other papers referred to in the above papers which would be valuable and copies are being sought. All of the references of which I am aware which may be directly relevant to the status of the Black Sea porpoise populations are listed in the bibliography.

History of the fishery

The catching of small cetaceans in the Black Sea apparently began circa 1870 (Zemsky and Yablokov, 1974). The earliest record I have been able to obtain is from 1927, when a catch of 9 300 animals by Soviet fishermen was reported (Zemsky and Yablokov, 1974).

The available statistics suggest a maximum Soviet catch of 135 to 140 000 animals in 1938. Subsequently, the catch apparently declined, until the whaling stopped in all countries except Turkey in 1966. Available catch statistics for the USSR, Bulgaria and Turkey are given in Table 1; the numbered notes indicate the variety of sources from which they were drawn. No information is available on the magnitude of the Romanian catch, but Jelescu (1960, quoted in Mitchell, 1974) describes the fishing techniques.

There are 3 species of small cetaceans involved in varying degrees in this fishery. These are *Delphinus delphis*, the common dolphin, *Phocoena phocoena*, the harbour porpoise, and *Tursiops truncatus*, the bottlenose dolphin. The catch statistics are generally available only for all species combined, as shown in the notes. It is known, however, that the common dolphin, *D. delphis*, has historically been predominant in the catch. Note that the catch records from the fishery have historically been reported in centners – hundred of kilogrammes. The formal English name for this quantity is quintal, and it corresponds approximately to 220 lb. The 9 300 animals figure reported for 1927 is apparently based on a conversion of one animal to approximately 54 kg (Zemsky and Yablokov, 1974). Thus the 1927 catch was probably first reported as 5 022 centners or 502.2 metric tonnes. The origin of the figure of 54 kg as the average weight of each animal in the catch statistics is unknown to me. Its accuracy depends on both the species composition and the age and sex composition of the catch. As no other conversion factors are available this has been used throughout this report.

Two methods of harvesting are used, guns and nets. The gun method apparently has a very high loss rate of wounded animals. The loss rate with the net fishery is considered small (Zemsky and Yablokov, 1974). Turkey, the only remaining country pursuing this fishery, uses the gun method (Zemsky and Yablokov, 1974).

With these points in mind, it appears that the Soviet fishery reached a peak in 1938 and then declined steadily. Thus, the average pre-war catch is listed as roughly twice that of the average post-war catch. This decline in the catch occurred despite greatly increased effort, both in quantity and quality. For instance, after the war, aerial spotting planes were

Table 1. Estimated numbers of small cetaceans killed in the Black Sea, by nation and for all nations, for all species, in thousands. Figures in parentheses indicate average catch over the time period covered by the arrows

Year	USSR	Bulgaria	Turkey	All Nations
1927	9.3[1]			
1928	(66.)[1]			
1929				
1930				
1931				(250-300)[3]
1932				
1933				
1934				
1935				
1936				
1937				
1938	134.-140.[2]			
1939				
1940				
1941*	≈0[18]		> 0[19]	
1942*	≈0	1.7[11]	> 0	
1943*	≈0		> 0	
1944*	≈0		> 0	
1945*	≈0		> 0	
1946	(≈33.0)[4]			
1947				
1948				
1949				
1950				
1951			(157-185.2)[7]	
1952				
1953				
1954				
1955		31.0[6]		
1956				
1957				
1958				
1959				
1960			30.0-40.0[8]	
1961	46.5[5]			
1962	**[15]			
1963	**			
1964	** (5.6-7.4)[17]			
1965	**			
1966	***[14] 0.0[16]		3.7[13]	
1967	*** 0.0	***[17] 0.0[17]	3.9[9] 1.0[13]	
1968	*** 0.0	*** 0.0	37.4[9]	
1969	*** 0.0	*** 0.0		
1970	*** 0.0	*** 0.0		

Table 1. Estimated numbers of small cetaceans killed in the Black Sea, by nation and for all nations, for all species, in thousands. Figures in parentheses indicate average catch over the time period covered by the arrows (*concluded*)

Year		USSR		Bulgaria	Turkey	All Nations
1971	***	0.0	***	0.0		
1972	***	0.0	***	0.0	35.2[9]	
1973	***	0.0	***	0.0	129.5[9]	
1974	***	0.0	***	0.0		

* Indicates war years;
** Indicates summer season fishery restriction;
*** Indicates complete fishery restriction.

[1] (Zemsky and Yablokov, 1974).
[2] (Zemsky and Yablokov, 1974) maximum catch reported.
[3] (Zemsky and Yablokov, 1974) "Summary catch of all Black Sea countries" to compare with abundance estimate for the thirties from Arseniev, Zemsky and Studenetsskaya, 1973.
[4] (Zemsky and Yablokov, 1974) "(The catch) in 1946-66 ... hardly reached half of this number" referring to 1927-38 average of 66 000 dolphins.
[5] (Zemsky and Yablokov, 1974) apparently maximum catch by USSR since war years.
[6] (Zemsky and Yablokov, 1974) maximum catch by Bulgaria.
[7] (Danilevsky and Tyutyunnikov, 1968).
[8] Mitchell (1975) quoted in Zemsky and Yablokov, 1974.
[9] (Zemsky and Yablokov, 1974).
[11] (Zemsky and Yablokov, 1974).
[12] (Danilevsky and Tyutyunnikov, 1968).
[13] (Danilevsky and Tyutyunnikov, 1968).
[14] (Danilevsky and Tyutyunnikov, 1968).
[15] (Zemsky and Yablokov, 1974) summer fishery restriction as of 1 May 1966.
[16] (Zemsky and Yablokov, 1974) catch effectively zero, amounting to "several dozens a year only".
[17] (Zemsky and Yablokov, 1974).
[18] (Zemsky and Yablokov, 1974).
[19] (Danilevsky and Tyutyunnikov, 1968).

introduced, which increased gear effectiveness (Zemsky and Yablokov, 1974). It does not appear, further, that any respite which may have occurred during the war benefited the porpoise populations appreciably. The catch of 5 600-7 400 animals per year reported for 1964 to 1966 represents a major collapse of the fishery (Danilevsky and Tuyutyunnikov, 1968). Accompanying this there has apparently been a marked change in the composition of the catch, by age, sex and species. It seems that earlier the catch was roughly equally divided between the sexes. In the 1963 and 1964 seasons the catch was composed of 70-75 % young, and pregnant or nursing females. This may have been associated with an extension of the fishing grounds (Danilevsky and Tuyutyunnikov, 1968). Similarly, the predominant species in the catch changed from *D. delphis* (80-90 %) to *P. phocoena* (Danilevsky and Tuyutyunnikov, 1968).

Note that *P. phocoena* is a small animal, with a maximum length of 167 cm for males and 180 cm for females (Tomilin, 1967). The maximum weight appears to be around 56 kg (Danilevsky and Tuyutyunnikov, 1968). This compares with maximum lengths of the order of 2 and 3 m for *D. delphis* and *T. truncatus*, respectively.

Referring again to Table 1, the Turkish fishery as reported is obviously important, and especially now when stocks are probably reduced. Despite the upheaval during the second world war, and the cessation of the Soviet fishery, the Turkish fishery continued (Danilevsky and Tuyutyunnikov, 1968). In addition, the use of guns means that the loss rate is high. In the period 1951-56 the average annual catch exceeded the maximum Soviet annual catch in 1938. Similarly, the reported catch in the last 2 years has approached that 1938 maximum. These data together with the high loss rate, suggest either an extremely intense fishery on a locally greater abundance of porpoise, or

Table 2. **Population size estimates in thousands, their natural logarithm, and percent change between years, after Zemsky and Yablokov, 1974.**

Year	*Tursiops*			*Delphinus*			*Phocoena*			Total		
	Pop. ('000)	Nat. log.	% Change	Pop. ('000)	Nat. log.	% Change	Pop. ('000)	Nat. log.	% Change	Pop. ('000)	Nat. log.	% Change
1967	65.7	4.19	+ 9.1	145.6	4.98	– 80.6	23.3	3.15	+ 25.3	234.6	5.46	– 44.9
1968	71.7	4.27	+ 91.1	28.3	3.34	– 7.1	29.2	3.37	– 58.2	129.2	4.86	+ 35.8
1969	137.0	4.92	– 73.0	26.3	3.27	+457.0	12.6	2.50	+100.8	175.5	5.17	+ 18.5
1970	37.0	3.61	+280.5	146.5	4.99	+ 94.3	24.5	3.20	– 25.3	208.0	5.34	+113.4
1971	140.8	4.95	– 19.4	284.7	5.65	– 11.8	18.3	2.91	– 19.7	443.8	6.10	– 14.6
1972	113.5	4.73	– 72.7	251.0	5.53	– 16.0	14.7	2.67	+126.5	379.2	5.94	– 27.4
1973	31.0	3.43		211.0	5.35		33.3	3.51		275.3	5.61	– 15.1
1974		–			–			–		(233.7)		
Mean	85.24		91.0	155.77		111.1	22.21		59.3	263.66		45.0
SDEV	45.46			102.24			7.64			112.35		
SD ERROR	17.18			38.64			2.89			42.46		
MEAN (LN)	4.30			4.73			3.05			5.50		
SDEV (LN)	0.61			1.00			0.36			0.43		
SER (LN)	0.23			0.38			0.14			0.16		

gross inaccuracies in the catch statistics. If the former, it does seem likely that a fishery of this magnitude could cause a reduction in the porpoise populations. This will be discussed in conjunction with the estimates of stock sizes.

With shifting species and age and sex composition it is unlikely that the numbers of dolphin per metric tonne of reported catch has remained constant. With the shift toward *P. phocoena* in the latter part of the fishery the average weight probably declined and hence the estimates of numbers killed are probably too low. In order to evaluate truly the impact of the fishery it is important to be able to determine the numbers of animals rather accurately.

Population sizes

The aggregate population size of all species of porpoise in the Black and Azov Seas was estimated for the thirties at 1.5 to 2.0 million animals (Arseniėv, Zemsky and Studenetsskaya, 1973; quoted by Zemsky and Yablokov, 1974).

In conjunction with the Soviet moratorium on harvesting porpoise, aerial surveys have been conducted twice a year since 1967. These have been designed to obtain estimates of the population sizes of the various species, and were apparently the basis of population estimates quoted in *Nature* (Anon., 1974). Since that article[1] additional information on these estimates of population size have become available in Zemsky and Yablokov, 1974. These authors provide estimates by species, as shown in Table 2. It can be seen that these estimates vary considerably from year to year and that no obvious trends are identifiable. In Fig. 1 the natural logarithm of the population

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[1] Note that in 1973 the population estimate is here given as 800 000, "three times the 1965 figure". I have no figure for 1965 and the 1973 estimate given in Zemsky and Yablokov, 1974, is 275 300 animals.

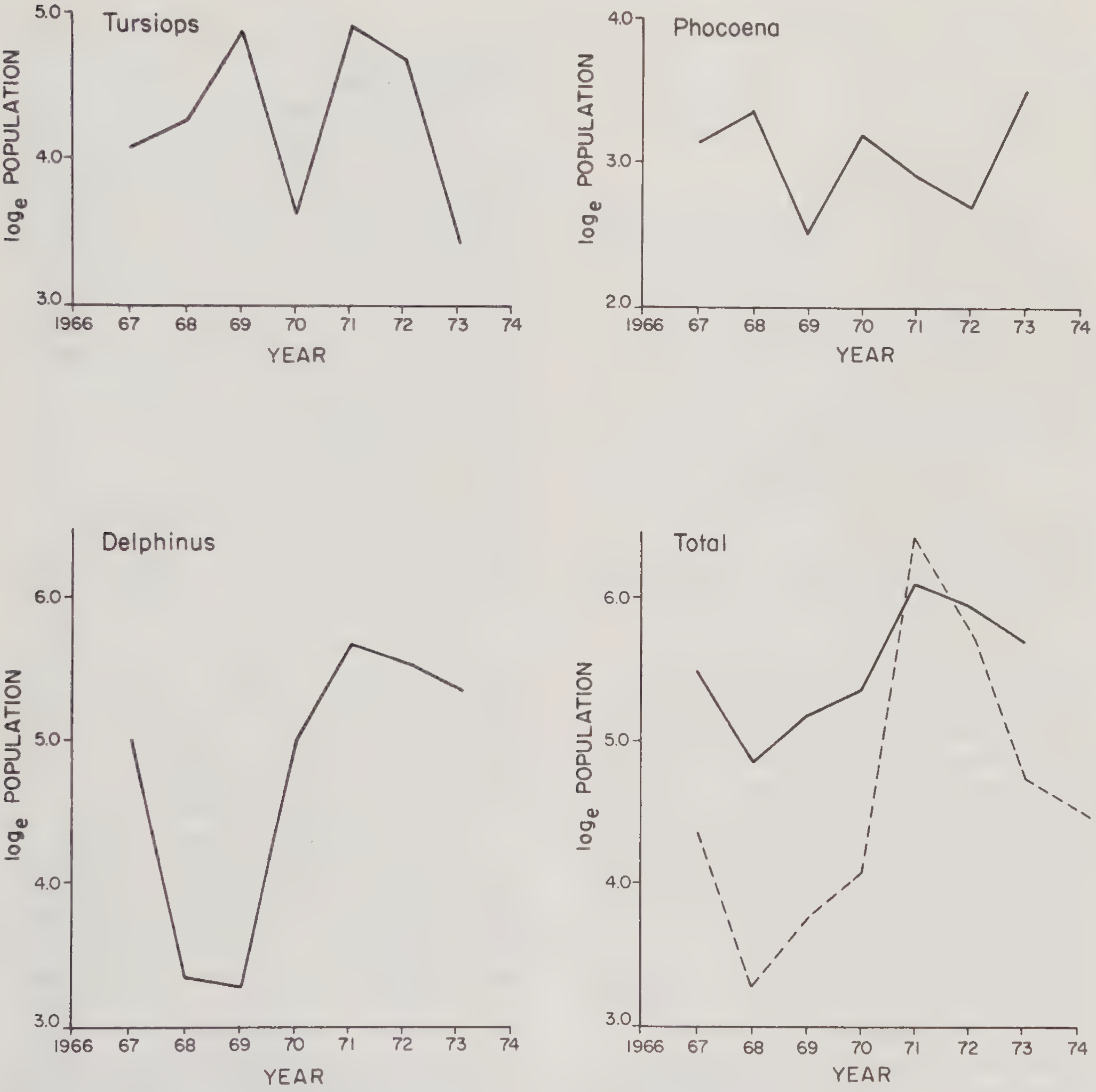

FIG. 1. – Logarithms of population size versus year for estimates of porpoise population size given in Zemsky and Yablokov, 1974, by species and total.

size estimates is plotted against time. It does not seem likely that cetacean populations, with their low reproductive rates and long lifespan, could experience fluctuations of this magnitude.

Some of the assumptions made in deriving these estimates are given. These include: (i) random distribution of porpoise; (ii) search of a path 3.0 km wide, and (iii) counting of one half of the animals in this path.

From personal coversations, I understand that:

- some large schools were seen and counted outside this path;
- the aircraft left the track line if the sighted school was large for a close fly by, and then returned to the track;
- the flight speed was 4 km/min;
- the area of the Black Sea inhabited by porpoise is 413 000 km^2;
- there are no small cetaceans in the Azov Sea (because of pollution), and
- the same route-march or trackline was followed on each of the surveys.

The location of this track is not given. It is not known how the results from the 2 surveys were combined each year.

Several comments are given in Zemsky and Yablokov (1974) about these estimates of population size. The estimates of the *Delphinus* population size are considered more reliable than those for *Phocoena* and *Tursiops*, because *Delphinus* is a more pelagic animal and the other 2 more inshore.

The high variability of these estimates, even for the more pelagic *Delphinus* population, appears most likely due to a failure to meet the assumption of randomness of the spatial distribution of the populations. Some information on the biology of these 3 species is of interest here. As mentioned in Zemsky and Yablokov (1974), *Phocoena* and *Tursiops* are generally found nearer shore than *Delphinus*. Sokolov (1971) referring to Kleinenberg (1956) describes *Tursiops truncatus* as feeding generally on benthic organisms, fairly near shore. It is restricted in distribution to the northern and eastern shores of the Black Sea (Tomilin, 1967). Sokolov also describes *Phocoena phocoena* as being a benthic fish feeder in coastal waters, but also a pelagic feeder in deep water. This species also feeds on anchovy-like fish when these occur in dense schools. This pelagic feeding is apparently most important in the spring and autumn (Tomilin, 1967). It is thought that *P. phocoena* feeds extensively on the Azov anchovy as it migrates from the region around the Caucasus Mountains north through the Kerch Strait into the Azov Sea. Danilevsky and Tyutyunnikov (1968) suggest also that *P. phocoena* winters on the Anatolian coast (West Turkey) and that it does not enter the Azov Sea. This latter point was also suggested by Yablokov (pers. comm.), citing pollution levels.

In distinction to these other 2 species, *Delphinus delphis* is a pelagic animal, feeding primarily on anchovy (*Engraulis encrasicholus*) and sprat (*Spratella spratus phaleriza*). Tomilin (1967) suggests that *D. delphis* feeds on local concentrations of these fish. Congregations of this porpoise will form over a concentration of fish for periods of 1 to 2 months. These 2 food species apparently spawn at different seasons, dispersed over the Black Sea, but form dense concentrations in the non-spawning season. The anchovy is a summer spawner and the sprat a winter spawner.

This biological background allows the assumption of random distribution to be evaluated. First, the assumption that *T. truncatus* and *P. phocoena* are distributed over the whole Black Sea, let alone randomly, appears questionable. It would seem necessary to obtain a better understanding of the area inhabited at the time of the survey. However, the assumption of these species being distributed over the whole area should result in a systematic bias, not in high variability. Second, the large concentrations of *D. delphis* feeding on the anchovy during the summer (the time of the surveys) will tend to increase the variability of the resulting estimates. As the track lines were not randomly placed this could also result in a possible bias in the estimates. This aspect could be evaluated further by examining the variability between the surveys within a year.

The accurate determination of the area inhabited is important to avoid a consistent bias in the resulting population estimates. Similarly, the accurate determination of the path effectively searched is important. The assumption of seeing one half of the animals within a 3 km path implies an effective path width of 1.5 km, or 0.75 km on a side. One interpretation of this is that the number of sightings made is the same as would have been made if a path 0.75 km on a side had been inspected completely.

Using this figure, one obtains the proportion of the area effectively searched as (8 000 × 1.5/413 000) = 0.029. Thus the number of animals sighted would be divided by this fraction to obtain the total population estimate.

This assumed path width can be checked against 2 other examples. Tomilin (1967) reports on observations made from an aeroplane in the late thirties, referring to Tsalkin (1936-38) and Golenchenko (1939). The sources of these references are not available. Flying at a speed of 130-180 km/h and at 200-500 m altitude, Tomilin suggests it is possible to see dolphin schools up to a maximum distance of about 7 km. He also reports that "most convenient" observation can only be made if the aircraft flies directly over or within approximately 1.5 km of the school. Tomilin notes that visibility deteriorates markedly if the sea state exceeds Beaufort 2. The assumption made about visibility is not inconsistent with these values, although perhaps soewhat conservative.

The second comparison is with figures given in Smith (1975). In an aerial survey in the eastern tropical Pacific in early 1974, the distance of sighting of each school was recorded. An average distance at which schools were sighted of 1.4 km was reported. Following Seber (1973) this average sighting distance can be interpreted as the effective path search on 1 side of the aeroplane.

This can be compared with the value of 0.75 km computed above, suggesting that the visibility in the Black Sea surveys is much less than that in the eastern tropical Pacific survey, or that one or more of the assumptions listed above are false.

Status of the stocks

A simple statistic which can be used to evaluate the impact of harvesting on a population is the crude exploitation rate, the ratio between the total number harvested and the total population size. In the Black Sea porpoise harvesting, the kill is not generally available by species, so it is necessary to compute this ratio for all stocks taken together.

In the thirties the total size of all stocks was estimated at 1.5-2.0 million. Comparing this to the estimated kill in 1936 of 0.25-0.36 million, one obtains a crude exploitation rate in the range of 12.5-20.0 %.

It is difficult to choose a most probable population size from the estimates given in Zemsky and Yablokov. However, if the general range of the estimates of 129 200-444 000 animals is reasonable, the current exploitation rates due to the Turkish kill can be computed. The estimates of the Turkish kill in this decade vary from 35 200-130 000 animals per year. These estimates suggest crude exploitation rates of 7.9-100.8 %. The observation that the Turkish harvesting has continued at high levels in 1973 and 1974 suggests that the population estimates are probably in the high end of the range.

Beyond these crude analyses there is little that can be said about the status of the stocks. The problems with the available estimates of population size, and probably also with the kill estimates, preclude a consistent understanding. It would appear necessary to refine both of those statistics, but especially the population size estimates. As discussed above, this latter would be possible by better determining both the area inhabited at the time of the survey and the effective path width searched.

Summary

I have assembled and reviewed what is available to me on the status of the Black Sea small cetacean populations. It is apparent that a fishery directly on these animals has reduced their abundance to marginal levels. By 1966 this reduction was sufficient to cause management action to be taken in some countries. The kill was probably excessive at the height of the fishery (12.5-20.0 %), and may still be so today (7.0-100.8 %).

However, the information on numbers killed and on numbers in the population is not sufficiently precise to allow for definite statements. Perhaps the most telling observation is that the numbers of small cetaceans in the Black Sea has declined substantially.

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STAUFFER AND CHARTER: 1981–82 NORTHERN ANCHOVY SPAWNING BIOMASS
CalCOFI Rep., Vol. XXIII, 1982

THE NORTHERN ANCHOVY SPAWNING BIOMASS FOR THE 1981–82 CALIFORNIA FISHING SEASON

GARY D. STAUFFER AND RICHARD L. CHARTER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

The biomass of the central subpopulation of the northern anchovy during the 1981 spawning season is estimated to be 2,803,000 short tons, based on the larva census method. Anchovy stock was surveyed over its geographic range on four cruises during the six-month period from January to June. The anchovy larvae in the plankton samples were sorted, counted, and measured, and the data were summarized to form larva census information for estimating the anchovy spawning biomass. The resulting 1981 estimate of 2,803,000 tons is approximately 58 percent greater than the 1980 estimate of 1,775,000 tons. The optimum yield for the central subpopulation in the 1981-82 fishing season is 601,000 short tons, as specified by the yield formula given in the Pacific Fishery Management Council's Northern Anchovy Fishery Management Plan. Within the U.S. 200-mile Fishery Conservation Zone, the optimum yield is 420,700 tons.

RESUMEN

La biomasa de la subpoblación de *Engraulis mordax* durante la temporada del desove en 1981 se calculó ser de 2,803,000 toneladas cortas, basado en el método de censo de larvas. La existencia de anchoveta fue reconocida durante cuatro cruceros por toda su extensión geográfica, durante un período de seis meses entre enero y junio. Las larvas de anchoveta en las muestras de plancton fueron separadas, contadas, y medidas, y los datos fueron resumidos para formar la información del censo de larvas para estimar la biomasa de desove de anchovetas. La estimación resultante para 1981 de 2,803,000 toneladas es aproximadamente el 58 por ciento más que la de 1980, de 1,775,000 toneladas. El rendimiento óptimo para la subpoblación central durante la temporada de pesca en 1981–82 es 601,000 toneladas cortas, especificado por la fórmula de rendimiento presentada por el Pacific Fishery Management Council en su Plan de Administración de la Pesquería de Anchoveta del Norte. Dentro de las 200 millas que abarca la Zona de Conservación de la Pesquería de los EE.UU., el rendimiento óptimo es 420,700 toneladas.

INTRODUCTION

The harvest plan for northern anchovy, *Engraulis mordax,* in California is specified in the Pacific Fishery Management Council's (PFMC) Northern Anchovy Fishery Management Plan (FMP), first implemented in 1978. The optimum yield for the U.S. fishing season is set according to the optimum yield formula given in the FMP and based on the current estimate of the spawning biomass. The purpose of this annual report, the fourth in a series, is to document the 1981 estimate of the spawning biomass of northern anchovy for the 1981–82 California fishing season. The 1981 biomass estimate is derived by the larva census procedure first developed by Smith (1972) and documented in Appendix I of the Anchovy FMP (PFMC 1978). Stauffer and Parker (1980) later developed the calibration for an annual larva census from the six-month winter-spring larva census. The 1981 anchovy larva data were collected on four cruises during winter and spring in the 1981 California Cooperative Oceanic Fisheries Investigations (CalCOFI) egg and larva survey. This survey was directed by the National Marine Fisheries Service, Southwest Fisheries Center (SWFC). Other agencies cooperating in the multicruise survey were Scripps Institution of Oceanography (SIO), Instituto Nacional de Pesca, Mexico (INP), and National Ocean Survey (NOS). Samples from Mexican waters were taken by permission of the Secretaria de Relaciones Exteriores under diplomatic note numbers 315052, 315576, 315611, 315984, and 316422.

LARVA SURVEY

The 1981 egg and larva survey of the central subpopulation of the northern anchovy was part of the 1981 triennial CalCOFI survey of the California Current region. The 1981 CalCOFI survey comprised six multiship cruises and sampled CalCOFI stations from line 60 at 38°N off San Francisco to line 137 at 25°N off central Baja California, Mexico, out to station 90—160 to 240 nautical miles offshore (Figure 1). To survey and estimate the spawning biomass of the central subpopulation of northern anchovies by July 1, 1981, as required by the FMP, we processed and analyzed plankton samples from only eight of the twenty-four CalCOFI regions (4, 5, 7, 8, 9, 11, 13,

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[Manuscript received February 12, 1982.]

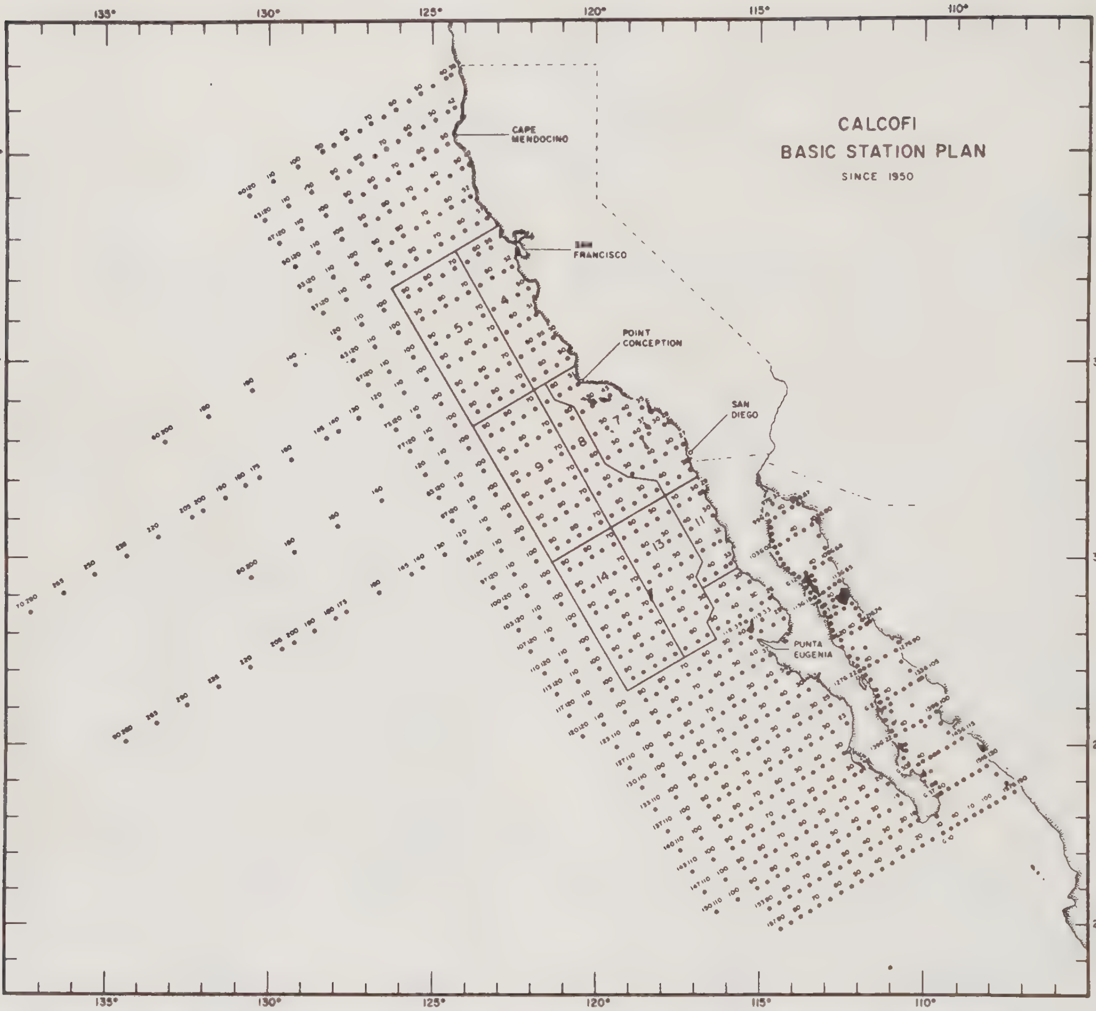


Figure 1. CalCOFI basic station plan. The geographic range of the central subpopulation of northern anchovy is within the eight numbered regions.

and 14) and from the four cruises conducted in the winter and spring. Approximately 130 CalCOFI stations were routinely occupied per cruise within these eight regions. As outlined in Figure 1, these geographic regions coincide with the range of the central subpopulation (Vrooman et al. 1980). The four winter and spring cruises covered the major portion of the anchovy spawning season (Stauffer and Parker 1980).

The anchovy survey cruises were scheduled at approximately six-week intervals beginning in early January (Table 1). Each cruise was about four weeks long. The January cruise was conducted over CalCOFI lines 110 through 60 by the R/V *David Starr Jordan* from January 7 to February 1. The second cruise,

TABLE 1
Schedule of the 1981 Egg and Larva Cruises

Cruise number	Cruise month	Survey quarter	Vessel name	Date	CalCOFI area
8101	January	Winter	*Jordan*	1/7-2/1	Lines 110 to 60
8102	February	Winter	(1) *Jordan*	2/12-3/10	Lines 110 to 60 within regions 4,7,8,11, and 13
			(2) *New Horizon*	2/12-3/8	Lines 60 to 110 within regions 5,9, and 14; lines 113 to 130
8104	April	Spring	(1) *Jordan*	3/31-4/27	Lines 110 to 100 in region 11; lines 97 to 60
			(2) *New Horizon*	4/7-4/28	Lines 100 to 133
8105	May	Spring	(1) *Jordan*	5/18-6/13	Lines 90 to 110
			(2) *New Horizon*	5/19-6/8	Lines 87 to 60

8102, was run with two ships, *Jordan* and R/V *New Horizon*, beginning February 12 and finishing March 10. The cruise plan for the *Jordan* included an egg survey of CalCOFI regions 4, 7, 8, 11, and 13 to estimate the anchovy biomass by the egg production method (Parker 1980). Stormy weather in February prevented the ship from surveying the stations in region 9 during cruise 8102. The first cruise of the spring quarter, 8104, began March 31 and ended April 28. The *Jordan*, conducting a second egg survey in regions 7, 8, and 11, occupied inshore stations on lines 110 to 100 and all routine stations on lines 97 to 60. The *New Horizon* surveyed the southern lines beginning with line 100, duplicating occupancy of region 11. The last cruise, 8105, began May 18 and ended June 13. The *Jordan* surveyed from lines 90 to 110, the *New Horizon* from lines 87 to 60.

The plankton samples were collected and processed with methods identical to the 1979 and 1980 surveys reported by Stauffer (1980) and Stauffer and Picquelle (1981). The plankton was sampled with a CalCOFI bongo net towed at a 45° angle from a maximum depth of 200 meters (Smith and Richardson 1977). The plankton samples from the starboard half of the bongo net were sorted. All of the plankton in a sample was sorted if the station was beyond 200 miles from shore or if the plankton volume was less than 26 ml; otherwise, a 50 percent aliquot of the sample was sorted. In all, 534 samples were collected and processed. Nineteen stations in region 11 were occupied twice during cruise 8104. The larva counts for these paired samples were averaged for the cruise. Because cruise 8105 ended June 13, time was too short to sort all the plankton samples for the July 1 deadline. Therefore, samples were not sorted for the stations in region 5 offshore of central California—a region with few anchovy larvae in May in the past. The larva data were entered into the computerized CalCOFI data management system where the data are edited, filed, processed, and summarized into larva census values for winter and spring quarters.

SURVEY RESULTS

The geographic distribution of anchovy larvae in 1981 has expanded somewhat farther offshore compared to the past three years. The number of larvae per station was low in the January cruise. The number of larvae per station in the February-March cruise increased tenfold over the January samples. The peak occurred in the April cruise, with the number of larvae 50 percent greater than in the February-March cruise. By May-June the number of larvae per station had decreased to a level similar to that in January. As shown in Figure 2, larvae in northern regions 4 and 5 were most abundant in the winter quarter cruises. Off Baja California, anchovy larvae were most abundant during March and April. Few larvae were taken there in the January and June cruises. The Southern California Bight, represented by region 7, contained the largest portion of the anchovy larvae. For the first time since 1975, a number of anchovy larvae were found in offshore region 9 during the April cruise. Unfortunately, stations in region 9 were not occupied during the February-March cruise. The large size of the larvae in region 9 suggests that the larvae were relatively old and were probably carried offshore by the California Current and upwelling plumes arising off central California. The first major upwelling of the 1981 season occurred from March 26 to April 9 off central and southern California (A. Bakun, Pacific Environmental Group, pers. comm.).

Of the 255 stations occupied in the winter quarter, 56 percent, or 143 contained anchovy larvae. For the spring quarter, 51 percent, or 134 out of 260 stations contained anchovy larvae. The larva census compiled for the eight regions of the central subpopulations is 11,127.4 × 10^9 larvae for the winter quarter and 14,164.3 × 10^9 larvae for the spring quarter. The combined winter-spring larva census, L_{WS}, is 25,921.7 × 10^9 larvae (Table 2).

TABLE 2

Estimated Larval Abundance (10^{12} larvae) for the Central Subpopulation from Appendix I, Table 2, FMP

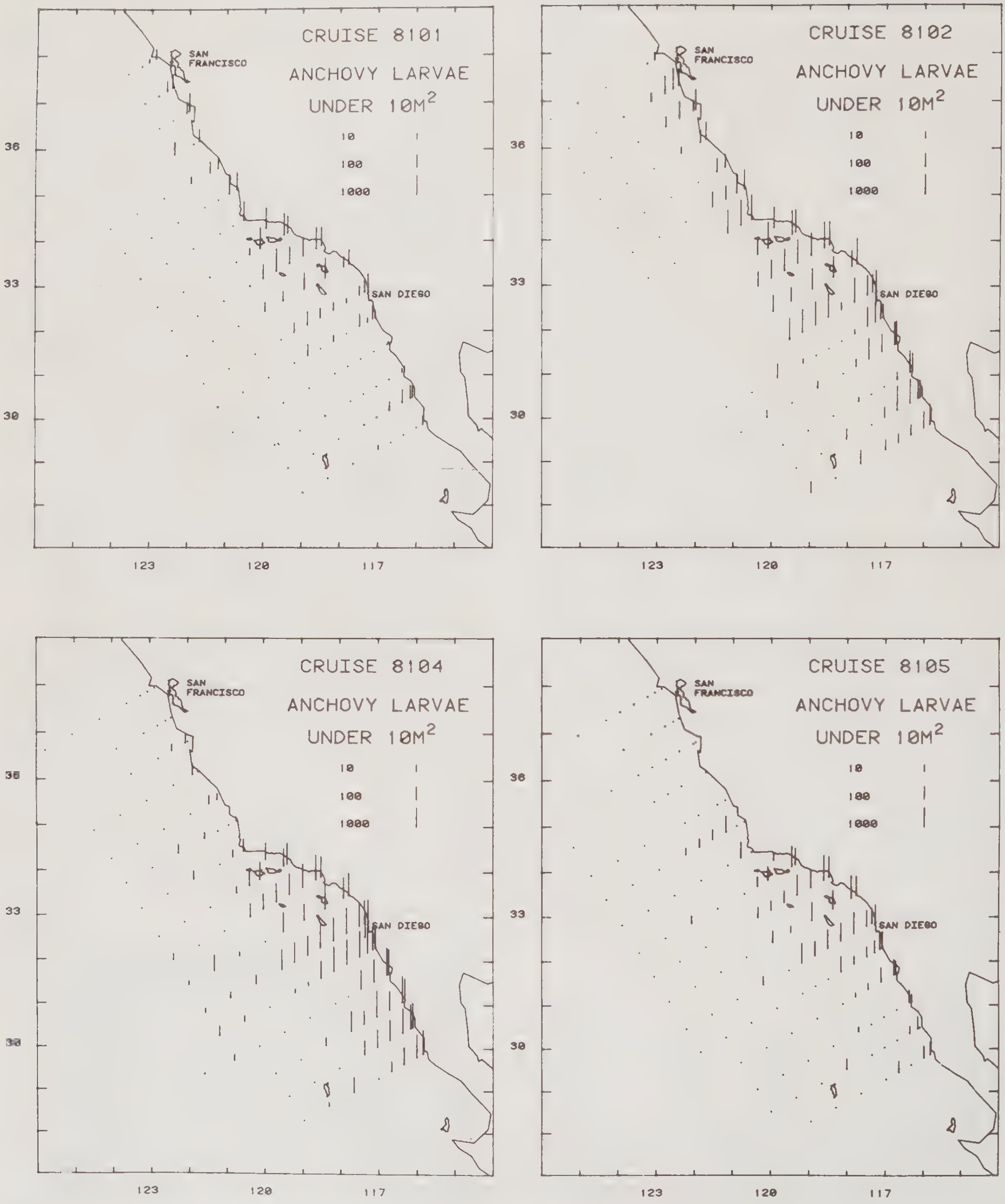
Year	Winter	Spring	Winter & spring	Annual	Spawner biomass in millions of short tons
1951	.298	.690	.988	1.841	.180
1952	.407	.457	.864	1.600	.156
1953	1.210	.373	1.583	5.208	.510
1954	4.469	.988	5.457	7.838	.768
1955	5.588	1.709	7.297	8.618	.845
1956	1.911	1.206	3.117	4.944	.485
1957	5.954	4.308	10.262	11.960	1.172
1958	8.114	5.236	13.350	15.087	1.479
1959	6.341	8.155	14.496	15.440	1.514
1960	7.552	7.547	15.099	15.713	1.540
1961	.992	6.714	7.706	11.827	1.159
1962	4.814	23.567	28.381	30.478	2.986
1963	17.377	24.818	42.195	43.407	4.254
1964	8.941	14.383	23.324	29.599	2.901
1965	19.155	22.690	41.845	47.540	4.659
1966	15.103	15.865	30.968	36.452	3.572
1969	19.756	6.538	26.294	30.594	2.998
1972	8.213	14.335	22.548	28.373	2.781
1975	29.754	4.071	33.825	36.768	3.603
1978	6.704	4.184	10.888	13.306	1.304
1979	6.546	9.124	15.670	17.580	1.723[1]
1980	—	—	—	18.110	1.775[2]
1981	11.127	14.164	25.292	28.603	2.803[3]

Spawner biomass in tons is calculated from annual larvae abundance; spawner biomass = 9.8 × 10^{-8} × larvae abundance, from Smith 1972.

[1] Stauffer and Parker 1980

[2] Stauffer 1980

[3] Stauffer and Picquelle 1981.


CRUISE 8101
ANCHOVY LARVAE
UNDER 10M²
10
100
1000
SAN FRANCISCO
SAN DIEGO
36
33
30
123
120
117
CRUISE 8102
ANCHOVY LARVAE
UNDER 10M²
10
100
1000
SAN FRANCISCO
SAN DIEGO
36
33
30
123
120
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CRUISE 8104
ANCHOVY LARVAE
UNDER 10M²
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SAN FRANCISCO
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CRUISE 8105
ANCHOVY LARVAE
UNDER 10M²
10
100
1000
SAN FRANCISCO
SAN DIEGO
36
33
30
123
120
117

Figure 2. Occupied stations for the 1981 cruises, and geographic distribution of anchovy larvae for the central subpopulation in the winter and spring. The vertical bars represent the logarithm of the number of larvae under 10 m² of sea surface.

BIOMASS ESTIMATE

The larva census estimates of anchovy biomass for the years 1951–69 developed by Smith (1972) are based on annual larva census values. Stauffer and Parker (1980) expanded the winter-spring larva census to an annual larva census, L, with the regression equation,

$$L = 1.062\, L_{WS} + 1{,}743 \times 10^9.$$

The equation is based on larva census data for 1951–75 summarized by CalCOFI regions as outlined in Figure 1. From this equation, the 1981 annual larva census is $28{,}602.7 \times 10^9$ larvae. The estimate of the 1981 spawning biomass, with Smith's (1972) equation,

$$B = 9.8 \times 10^{-8}\, L,$$

is 2,803,000 short tons. This is a 58 percent increase over the 1980 estimate of 1,775,000 tons, and is the third consecutive year with an increase in the biomass estimate since the 1978 low of 1,304,000 tons (Figure 3). The 1981 larva census values for the winter and spring quarters and the resulting biomass estimate are nearly identical to survey results for 1964 and, more recently, 1972.

OPTIMUM YIELD

The optimum yield for the 1981-82 fishing season for the estimated biomass of 2,803,000 tons is 601,000 tons based on the formula specified in the Northern Anchovy FMP (PFMC 1978). The optimum yield in the U.S. Fishery Conservation Zone (FCZ) is 70 percent or 420,700 short tons, The U.S. capacity to process anchovies, including live bait, is estimated to be 371,885 tons. The difference of 48,815 tons is available to joint ventures or to foreign fisheries within the U.S. FCZ as TALFF (Total Allowable Level of Foreign Fishing). The 1981–82 quota for the U.S. commercial fishery was set at 359,285 tons by National Marine Fisheries Service. However, the California Fish and Game Commission established a 150,000 short-ton limit on the amount of northern anchovy that could be processed by shore-based reduction plants in California because of the discrepancy between the 1980 estimates of biomass using the larva census method and the newly developed egg production method (Stauffer and Picquelle 1981).

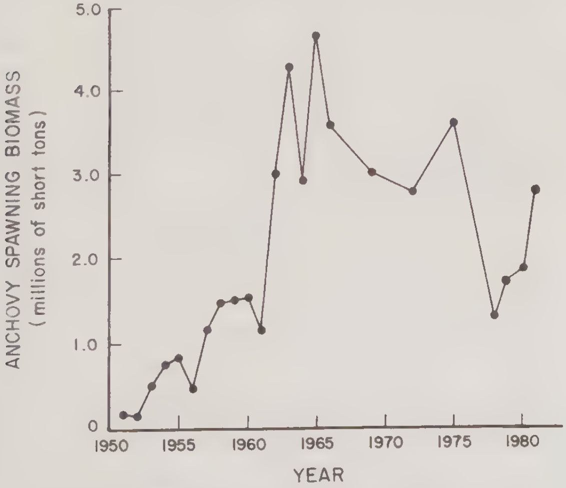

Figure 3. Estimated spawning biomass for the central subpopulation of northern anchovies, 1951–81.

ACKNOWLEDGMENTS

We thank many people for their efforts in collecting and processing the CalCOFI egg and larva data used in this estimation. They include Scripps Institution of Oceanography (SIO) plankton sorting group,Southwest Fisheries Center CalCOFI group, and crews of NOAA Ship R/V *David Starr Jordan* and SIO R/V *New Horizon*. We could not have accomplished this task without everyone's full cooperation and extra effort.

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ENERGETICS OF LOCOMOTION IN WARM-BODIED FISH

E. Don Stevens

Department of Zoology, University of Guelph, Guelph, Ontario
N1G 2W1, Canada

Andrew E. Dizon

National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96822

INTRODUCTION

Most fishes are poikilothermic—i.e. their body temperature is within a few degrees of ambient unless ambient is changing rapidly. The exceptions are certain sharks and true tunas. Little is known about the locomotion and energetics of warm-bodied sharks. Our review focuses on a few species of tunas but draws on information from other fish (especially salmonids) to fill in the gaps in our understanding.

Of interest here is a measure of the metabolic cost of producing known amounts of work per unit time; but there are problems with both sides of this equation, especially in the aquatic environment. Webb (30) has used a scheme similar to that in Figure 1 to show how total metabolic costs are partitioned. Since this approach is appropriate for sustained swimming in steady-state (i.e. oxygen supply keeping up with demand), especially when experiments are performed for short periods (hours), it is used here.

Energy input or metabolic cost has been successfully estimated by measuring oxygen uptake and calories ingested. We focus our discussion on estimates based on these measurements.

Other techniques for measuring metabolic costs have either been tried unsuccessfully or are yet to be tried. For example, few measurements have been made of CO_2 production in fish (15, 16) and none for tuna. Knowledge of heat exchange rates and excess temperature has permitted some specula-

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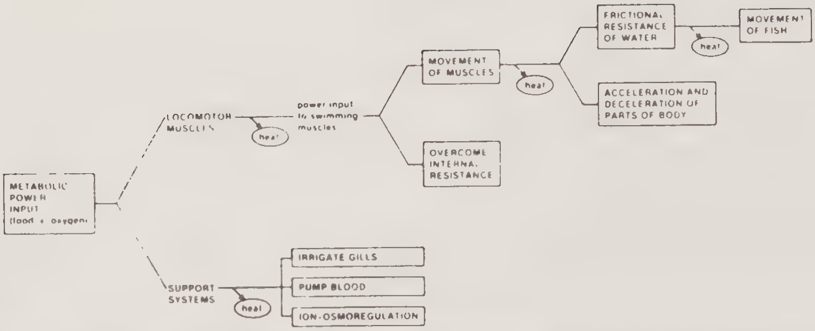
METABOLIC POWER INPUT (food + oxygen)
LOCOMOTOR MUSCLES
heat
power input to swimming muscles
MOVEMENT OF MUSCLES
heat
FRICTIONAL RESISTANCE OF WATER
heat
MOVEMENT OF FISH
ACCELERATION AND DECELERATION OF PARTS OF BODY
OVERCOME INTERNAL RESISTANCE
SUPPORT SYSTEMS
heat
IRRIGATE GILLS
PUMP BLOOD
ION-OSMOREGULATION

Figure 1 Schematic of energy distribution to components involved in propulsion at sustained swim speeds.

tion about energetics (19), but little is known about how heat exchange rates change during swimming. Guppy and co-workers have studied biochemical adaptations of burst swimming but not of sustained swimmming (11).

Known amounts of work per unit time have never been measured for water breathers. Metabolic costs are usually related to swimming velocity. Some workers have used arbitrary estimates—e.g. measured oxygen uptake or temperature after "feeding frenzy." Others have measured time to swim a specific distance when the tuna is controlling its own speed. Still other estimates are based on hydrodynamic theory, which is used to estimate the work to overcome drag or produce the thrust necessary to swim at a particular speed.

We review recent contributions on tuna energetics based on measurements of oxygen uptake, bioenergetic calculations from feeding and growth rates, and hydrodynamic calculations. We discuss the partitioning of this energy in tunas. Finally, we compare the cost of locomotion in tunas to that in birds and mammals and comment on the adaptive advantage of being warm-bodied.

We stress the two main differences between locomotion on land and in water. First, water as a medium offers much resistance (i.e. it has high viscosity and high density) so that almost all locomotive work goes to overcome drag. Second, water supports the fish's weight, so that almost no work goes to overcome gravity. Warm-bodied fishes swim continuously; thus inertial losses are small when they swim at constant velocity.

TOTAL COST OF LOCOMOTION

Estimates of the total cost of locomotion are based on measurements of the gross cost. There have been many attempts to calculate net cost by estimating maintenance costs (i.e. of ion-osmoregulation, of obtaining oxygen from the medium, and of delivering oxygen to cells that need it). We first discuss total and then net costs.

Oxygen Uptake Used to Estimate Total Cost of Locomotion

The only measurements of oxygen uptake in free-swimming tunas at known swim speeds are those of Gooding et al (10). In their experiments, groups of two to six skipjack tuna (*Katsuwonus pelamis*) were placed in large respirometers (4.6 m diameter, 1 m deep; or 2.4 m diameter, 0.6 m deep) where oxygen depletion and swim speed were measured. Thus over the long term the experiment provided a measure of total oxygen uptake at known swim speeds (i. e. in cases for which the fish maintained the same velocity for hours). Swim speed was controlled by the fish and not the experimenters. The data appear in Figure 2. Three aspects of their results are unique. First, there was no statistically demonstrable effect of body weight among oxygen uptake rates for skipjack tunas over a weight range of 0.60–4.0 kg. Second, the metabolic rate at any speed over the range studied (i.e. 0.9–2.2 $l{\cdot}sec^{-1}$) (l=body lengths) was higher than that of any other fish species studied. For example, at 1 $l{\cdot}sec^{-1}$, oxygen uptake in the skipjack is 469 $mgO_2{\cdot}kg^{-1}{\cdot}h^{-1}$ whereas in eight other species it ranged from 90–300 (1). At 2 $l{\cdot}sec^{-1}$ oxygen uptake in skipjack is 603 $mgO_2{\cdot}kg^{-1}{\cdot}h^{-1}$ whereas in the eight other species it ranged from 200–440 (1). These data show that tuna are less efficient than other fish species when swimming at these speeds and that the obvious streamlining of tunas does not lead to an obvious saving of total metabolic costs at swim speeds about 1–2 $l{\cdot}sec^{-1}$. "Presumably, the evolution of skipjack tuna (like that of fast cars) has involved sacrifice of energetic efficiency at low speeds in favour of increased efficiency at high speeds, permitting a dramatic increase in maximum attainable speed" (10).

Unfortunately, there are no oxygen uptake measurements of tunas swimming at higher speeds. However, in skipjack tuna immediately after capture at sea the median rate of 15 measurements was 1300 $mgO_2{\cdot}kg^{-1}{\cdot}h^{-1}$ (range 900–2500) (10). Swim speed ranged from 2–5 $l{\cdot}sec^{-1}$. These measurements are important because they suggest the tuna's maximum aerobic scope. They are higher than any values for any other fish (or amphibian or reptile) under any exercise, temperature, or other experimental condition.

The third unique aspect of Gooding et al's data is the fact that the slope of the line relating log metabolic cost to swim speed is less than that for other fish. When the logarithm of metabolic rate is plotted versus swim speed, a straight line can usually be fitted to the data. The slope of this line for skipjack tuna is 0.21 (Figure 2) (10), less than that for the other eight species tabulated by Beamish (1). "The rate of increase in the logarithm of oxygen uptake with relative swimming speed is surprisingly similar among species despite obvious variation in methodology, size, and temperature and is reasonably well represented by a coefficient of 0.36. Thus for each increase in relative swimming speed of $l{\cdot}sec^{-2}$ there is a corresponding 2.3-fold eleva-

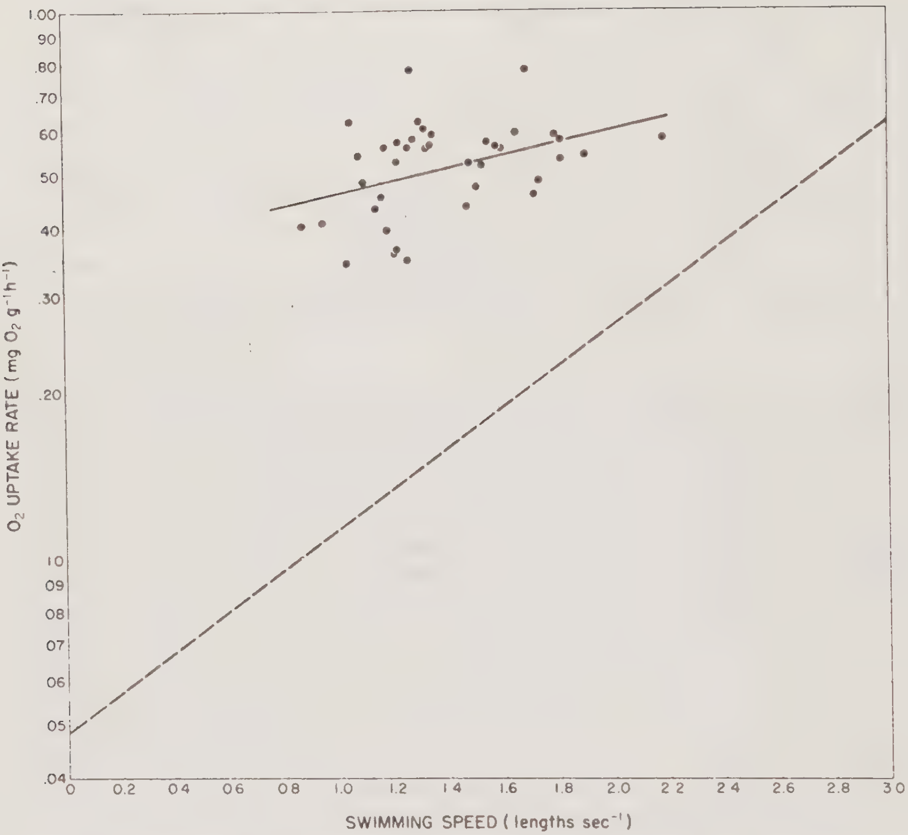

Figure 2 Relation between oxygen uptake and swim speed of skipjack tuna. The dashed line is for 1.8 kg sockeye salmon (2). Figure adapted from (10).

tion in metabolic rate" (1). But this coefficient is 0.21 for skipjack, involving only a 1.6-fold elevation in metabolic rate. The tuna becomes more efficient than the salmon at a speed of less than 5 $l \cdot sec^{-1}$, and tuna can sustain speeds greater than 5 $l \cdot sec^{-1}$, whereas salmon cannot (7).

NET COST OF LOCOMOTION

Calculation of the net cost of locomotion requires an estimate of basal metabolic rate (or at least the rate at zero activity). The major fraction of these costs is usually attributed to irrigation of the gills with water, circulation of the blood, and ion-osmoregulation.

Stevens (24) measured respiration in skipjack tuna restrained in a chamber. The average oxygen uptake was 692 $mgO_2 \cdot kg^{-1} \cdot h^{-1}$ and the mean of the lowest value recorded for each of five skipjack was 457 $mgO_2 \cdot kg^{-1} \cdot h^{-1}$. Clearly these values are not resting or basal and thus cannot be used to estimate net cost of locomotion. Brill (3) attempted to overcome the problem of obtaining resting values by measuring "stasis" metabolism (metabolism of restrained skipjack injected with a muscle relaxant, gallamine triethiodide, and then spinalectomized to stop all overt muscular movement). Smaller animals had higher mass-specific stasis metabolic rates. For a mass range of 0.32–4.7 kg, the relation was $M = 8431\ W^{-0.437}$, where M = oxygen uptake ($mgO_2 \cdot kg^{-1} \cdot h^{-1}$) and W = mass (g). Thus stasis metabolic rate for a 2 kg skipjack is 304 $mgO_2 \cdot kg^{-1} \cdot h^{-1}$ or about one half the value reported for a nonspinalectomized fish and about one half the value from the swimming fish when extrapolated to zero activity (529 $mgO_2 \cdot kg^{-1} \cdot h^{-1}$). We assume that this measurement is a reasonable estimate of the metabolic cost of the support systems in tuna at zero activity. Most evidence shows that these costs increase in proportion to swim speed.

Cost of Irrigating The Gills

The typical pattern of rhythmic movements of respiratory muscles to force water over the gills is not seen in tunas. Tunas, swimming with an open mouth, irrigate the gills by ram pressure. The literature on irrigation of the gills by open-mouth swimming has been reviewed (23).

Thus the metabolic cost of irrigating the gills is a small fraction (of the order of 1%) of total metabolic cost of swimming in tunas (i.e. it is about one order of magnitude less than that in fish irrigating their gills with buccal and opercular pumps).

Cost of Circulating The Blood

The cost of circulating the blood must be higher in tunas than in other fishes. The absolute cost must be higher because the metabolic rates are so high—i.e. because more oxygen must be delivered to the tissues. The relative cost is probably also high because of the unusual circulatory system of tunas. Tunas have elaborate counter-current heat exchangers that keep their body temperatures substantially higher than that of the water. The imposition of the heat-exchanger vascular beds in series with the typical vascular beds must result in a greater work load on the heart. The cost of circulation is estimated at 3.5% of total oxygen uptake at rest and 4.5% of total oxygen uptake at maximum activity in salmon (13). In tuna it is probably greater than 5%.

Cost of Ion-Osmoregulation

There are two elaborate studies on the metabolic cost of ion-osmoregulation in fish (8, 22). Both used euryhaline species and estimated the cost by measuring oxygen uptake at a variety of salinities. Costs increased exponentially with swimming speed, reaching 17% of total metabolism at maximum swim speed.

Thus the costs of maintaining the support systems during swimming as fractions of the total metabolic cost are probably about 1% to irrigate the gills, 5% to circulate the blood, and 15–20% for ion-osmoregulation.

METABOLIC COSTS BASED ON CALORIC INPUTS

Kitchell et al (14) constructed energy budgets for two species of tuna using the principles of bioenergetics in order to estimate the scope for growth.

Small Tropical Tuna

From (10), M (routine metabolic rate in $\mathrm{mgO_2 \cdot h^{-1} \cdot fish^{-1}}$) is $0.288 \cdot W^{1.08}$, where mass is in g. Thus for a 2 kg skipjack routine metabolic rate is 1058 $\mathrm{mgO_2 \cdot h^{-1}}$ or 86 $\mathrm{kcal \cdot day^{-1}}$. Given the caloric density of skipjack (1.46 $\mathrm{kcal \cdot g^{-1}}$), this is about 3.7% of total energy content per day. Measured values show that actual losses of energy content during 10 days starvation are 3.6% per day. Because this calculation is based on Gooding's estimate of routine metabolic rate, the result depends on body mass. However, because the exponent is small (0.08), changes with mass are small. The decrease in energy content per day is $2.012\ W^{0.08}$ (where mass is in g) or 3.2% for the smallest skipjack used by Gooding (0.32 kg) and 4.0% for the largest (4.7 kg).

Kitchell et al extended their calculations to estimate the energy required to account for observed growth rates of skipjack in the field. The observed growth rate is 0.7% mass per day or 10 $\mathrm{kcal \cdot fish^{-1} \cdot day^{-1}}$ for a 1 kg skipjack. In the laboratory small skipjack can consume food equivalent to 28–35% of their body $\mathrm{mass \cdot day^{-1}}$. Kitchell et al deduced that small skipjack (less than 7–10 kg) grow at rates substantially lower than maximal and thus appear limited by food availability and/or their efficiency as predators. Growth of large skipjack (greater than 7–10 kg) appears limited by the rate at which food can be consumed and physiologically processed. This upper limit appears to account for the upper size limit of skipjack observed in the field (25 kg). Observed growth rates in the field and maximum size in the field are concordant with a metabolic rate slightly more than twice the routine rate observed by Gooding (14), i.e. about $577 \cdot W^{0.08}$. For a 0.32 kg fish this is 915 $\mathrm{mgO_2 \cdot kg^{-1} \cdot h^{-1}}$; for a 2 kg fish it is 1060 $\mathrm{mgO_2 \cdot kg^{-1} \cdot h^{-1}}$; and for a 4.7 kg fish it is 1134 $\mathrm{mgO_2 \cdot kg^{-1} \cdot h^{-1}}$. All of these values are higher than rates measured at maximum sustained swimming speeds for any other species at any temperature. We can calculate the approximate speed for a particular mass when oxygen uptake $= 0.577\ W^{0.08}$ (i.e. when it is twice the routine rate measured by Gooding) by substituting into the original relation (10).

$$S = (22.35–2.558 \log W)\cdot W^{0.2831},$$

where S is speed in km·day^{-1} and W is mass in g. To estimate fuel used we convert metabolic rate to grams of fat used per day. Fuel economy (FE) can now be calculated by dividing km travelled per day by fat used per day. $FE = (4511–516.4 \log W)\cdot W^{-0.7969}$, where FE is in km·g fat^{-1} when swimming at speeds equivalent to twice the routine rates.

Thus the 0.32 kg tuna travels 82 km·day^{-1} using 2.52 g fat (32 km·g fat^{-1}) whereas the 4.7 kg tuna travels 142 km using 45.8 g fat (3.10 km·g fat^{-1}). Large tuna must consume and physiologically process ten times as much fuel to swim less than twice as far. For each doubling of mass, fuel economy is approximately halved, a relation analogous to that between the fuel consumption rates of small and large cars.

Pennycuick has made similar calculations for birds (20, 21). A 3 g hummingbird travels 880 km per g fat, whereas the larger bird, a 384 g pigeon, travels only 11.7 km per g fat. The 384 g pigeon and the 320 g skipjack get similar mileage. Similar calculations can be made for a 384 g white rat (29). At maximum speed (2.25 km·h^{-1}) it could travel 54 km at a total cost of 13.8 g fat·day^{-1}. These relations are summarized in Table 1.

Giant Bluefin Tuna

The approach of Kitchell can be applied to the largest tuna, the giant bluefin. This animal's oxygen uptake has not been measured, but we do know something about its feeding and growth rates. Giant bluefin arrive in Nova Soctia in July weighing about 350 kg. They gain about 20% in body mass (all fat) in about 60 days when fed a rate of about 4% body mass per day. The caloric content of the food, mackerel, also a scombroid, is probably about the same as that of the tuna. Assuming a caloric density the same as skipjack, then mass-specific metabolic rate is:

$$\frac{0.0227\ \text{kg}}{\text{kg·day}} \times 1000\ \frac{\text{g}}{\text{kg}} \times \frac{1.46\ \text{kcal}}{\text{g}} \times \frac{1\ \text{mgO}_2}{0.0034\ \text{kcal}} \times \frac{1\ \text{day}}{24\ \text{h}} = 406\ \text{mgO}_2\text{·h}^{-1}\text{·kg}^{-1}.$$

This is surprisingly similar to the maximum active rate for salmon extrapolated over two orders of magnitude: Active salmon metabolism = $(1.772 \times 385000^{0.888})/385 = 420$ mgO$_2$·h^{-1}·kg^{-1}. The speed at this metabolic rate extrapolated from the salmon equation is 1.53 l·sec^{-1}. This is slightly more than the observed speed (1 l·sec^{-1} or 3 m·sec^{-1}) for which the bluefin metabolic estimate is made.

We can also compare the giant bluefin's net cost to that of a similar-sized mammal (28). Net mammal metabolism is: $M = 760 \cdot W^{-0.4} = 760 \cdot 385^{-0.4} = 70.3\ \mathrm{mgO_2 \cdot kg^{-1} \cdot km^{-1}}$. The net cost for bluefin is almost exactly half the value for a mammal of equivalent mass. Thus the fuel economy of the tuna is twice that of the mammal (Table 1).

NET COSTS BASED ON THRUST AND DRAG ESTIMATES

Independent estimates of net energy costs can be made in a straight-forward manner from the thrust/drag relationships of a swimming fish (6, 7). These estimates can then be compared with the laboratory values from the respirometers. The estimates are made as follows: In steady-state swimming, total thrust force (dynes) equals total drag force (dynes). By first principles (30), drag force is $D = 0.5 \cdot S \cdot \rho \cdot V^2 \cdot C_D$, where S = wetted surface area ($\mathrm{cm^2}$), ρ = fluid density ($\mathrm{g \cdot cm^{-3}}$), V = velocity ($\mathrm{cm \cdot sec^{-1}}$), and C_D = coefficient of total drag. Similarly, thrust force is $T = 0.5 \cdot S \cdot \rho \cdot V^2 \cdot C_T$ where S = surface area of caudal fin ($\mathrm{cm^2}$), V^2 = lateral velocity of fin ($\mathrm{cm \cdot sec^{-1}}$), and C_T = coefficient of total thrust.

Power is the time rate of doing work, and work is the application of force through a given distance. But since the propulsion system is not 100% efficient, more power input is required for the power output necessary to propel a given fish at a given speed. Total aerobic efficiency is generally taken (30) as 0.2, which means of course that about 80% of the input power is lost as heat and does no usable work (Figure 1). Thus $P_i = (D \cdot V \cdot 10^{-7})/n$, and $P_i = (T \cdot V \cdot 10^{-7})/n$, where P_i = input power (watts) and n = total aerobic efficiency = 0.2. To this input power must be added the power necessary to fuel the nonswimming processes described in the previous section.

Table 1 The metabolic cost of locomotion of tunas compared to other endotherms of similar mass

Animal	Mass	Speed ($\mathrm{km \cdot day^{-1}}$)	Fat used ($\mathrm{g\ fat \cdot day^{-1}}$)	Fuel economy ($\mathrm{km \cdot g\ fat^{-1}}$)
Small endotherms				
Skipjack	320 g	82	2.52	32
Pigeon	384 g	1374	117	11.7
Rat	384 g	54	13.8	3.9
Large endotherms				
Bluefin	385 Kg	259	1237	0.21
Salmon[a]	385 Kg	397	1283	0.31
Mammal	385 Kg	259	2510	0.10

[a] Extrapolated from salmon data (2) at the maximum activity level

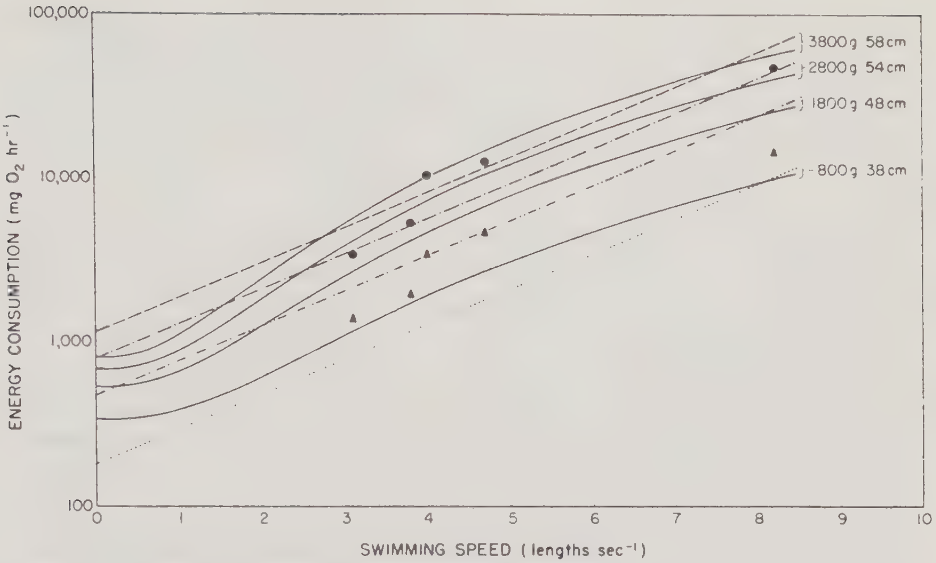

Figure 3 Comparison between measured oxygen uptake extrapolated to 8.5 *l*. sec^{-1} (broken lines) and the theoretically calculated power consumption based on hydrodynamic considerations (solid lines). Triangles (▲) are the theoretical power consumption based on an analysis of drag forces, and points (●) are based on an analysis of thrust forces for a 40 cm, 1003 g skipjack tuna (17). Figure adapted from (10).

Precise estimates of body surface area exist for many species of tuna, along with regression relationships based on length (18). Remaining are estimates of the coefficients of drag and thrust; these are the most questionable and subject to error. For the construction of the solid lines in Figure 3, a simple relationship was used (6,10). The simple drag model produces conservative values.

The measured oxygen-uptake relationship in Figure 2 extrapolated to 8.5 *l*·sec^{-1} compares well to the theoretical projections of energy consumption based on the simple drag model (Figure 3). Magnuson's (17) estimates of the theoretical power consumption of a 40 cm, 1003 g skipjack tuna, based on either model of thrust forces or based on an accurate estimate of total drag, are also presented in the figure. These compare well and are conservative, predicting even larger expenditures of energy.

THERMOCONSERVATION, LOCOMOTION, AND ENERGETICS IN TUNAS

The feature that most sets tunas apart from other fishes is the fact that they are warm-bodied. Is this fact related to locomotion and/or the energetics of locomotion? Arguments concerning the adaptive advantage of being warm relative to the water have been discussed in detail (27). Recently Stevens & Carey (25) developed a new argument.

Tuna are especially well adapted to sustain high speeds (they have many morphological features that reduce drag) rather than to achieve high burst speeds (which require low mass, and for which frictional resistance is less important). Yuen (31) reported a school of skipjack tuna that travelled 28 km in 107 min—i.e. fish 40–50 cm long can swim at speeds of about 10 $l \cdot sec^{-1}$ for at least an hour.

Stevens & Carey (25) argue that being warm-bodied confers an adaptive advantage because it increases the amount of oxygen that can be delivered to active cells. Passive diffusion of oxygen has a Q_{10} of about 1. The Q_{10} of transport of oxygen by myoglobin is higher, probably between 1.5 and 2 (E. D. Stevens, unpublished). Skipjack tuna muscle temperature changes with activity level, at least when we compare extreme activity levels. Tuna muscle has much red muscle that contains a high concentration of myoglobin. Thus the warmth may increase the rate at which myoglobin delivers oxygen to the mitochondria of active cells.

Although the above reasonably explains the advantage of warm muscle, it does not explain that of a warm stomach. Telemetric observations of free-swimming bluefin tuna (F. G. Carey, E. D. Stevens, and J. W. Kanwisher, unpublished data) show that these tunas increase stomach temperature after a cold meal and keep it warm for hours during digestion (stomach temperature 25–30°C, water temperature 12°C). In this case it seems that being warm-bodied confers an adaptive advantage because it permits an increase in the rate at which food can be physiologically processed.

All tunas, from the small tropical tunas to the giant bluefin, also have elevated brain temperatures. Brain temperature of skipjack increases from about 0.1°C to 4°C above ambient during rapid swimming (26).

Thus although being warm is what makes tuna unique among fishes, no single function can be attributed to the warmth. Tunas inhabit parts of the ocean where food is dilute and patchily distributed. They maximize energy gain by "gambling" large energy expenditures (high sustained activity) on the "expectation" of proportionately large energy returns (25, 27). Being warm is one aspect of this "gamble."

ACKNOWLEDGMENTS

We thank J. M. Renaud and J. Galbraith for comments on the first draft and Mary Anne Finkbeiner for transcribing the manuscript. One of us (E.D.S.) takes this opportunity to point out that the financial support for research on tunas provided by Fisheries and Oceans of Canada would not buy peanuts for a pet squirrel.

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OBSERVATIONS ON THE EARLY LIFE HISTORY OF THE MUSSEL BLENNY, *HYPSOBLENNIUS JENKINSI*, AND THE BAY BLENNY, *HYPSOBLENNIUS GENTILIS*, FROM SPECIMENS REARED IN THE LABORATORY

ELIZABETH G. STEVENS AND H. GEOFFREY MOSER
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center
La Jolla, California 92038

ABSTRACT

Two egg masses of the mussel blenny, *Hypsoblennius jenkinsi,* with attending males, were collected in Mission Bay, California, and incubated in the aquarium. After hatching, the broods of larvae were reared to the benthic juvenile stage on a diet of the rotifer *Brachionus plicatilus* and brine shrimp. Juveniles of one of the broods were maintained in the aquarium to the adult stage. On day 141 after hatching, one of the females produced a viable egg mass from which larvae hatched in 22 days. A single egg mass of the bay blenny, *Hypsoblennius gentilis,* was collected and incubated in a similar manner, producing larvae that were reared to a length of 6.7 mm. This paper describes the eggs and larvae of *H. jenkinsi,* including growth rate, and provides characters for distinguishing the larvae of this species from *H. gentilis* larvae.

RESUMEN

En Mission Bay, California, se recolectaron dos nidadas de huevos del blenio *Hypsoblennius jenkinsi,* junto con los machos que las atendían, para ser incubadas en al laboratorio. Las larvas eclosionadas se criaron alimentadas con el rotífero *Brachionus plicatilus* y el crustáceo *Artemia salina* hasta que alcanzaron la fase juvenil bentónica. Los juveniles de una nidada lograron alcanzar la fase adulta, y una hembra de 141 días efectuó una puesta de huevos de los cuales eclosionaron larvas a los 22 días. Una puesta de huevos del blenio *Hypsoblennius gentilis* que también se recolectó, fué incubada bajo las mismas condiciones, obteniéndose larvas que alcanzaron 6.7 mm de longitud. En este trabajo se describen los huevos y larvas de *H. jenkinsi,* incluyendo su índice de crecimiento, y se discuten los caracteres distintivos de las larvas de esta especie y de *H. gentilis*.

INTRODUCTION

The family Blenniidae is represented off California and Baja California by three species of the genus *Hypsoblennius: H. gentilis, H. gilberti,* and *H. jenkinsi* (Miller and Lea 1972). The behavior of these species has been studied by Stephens et al. (1970) and Losey (1968), but descriptions of their larvae have not been published. Eggs and larvae of an Atlantic species, *H. hentzi,* were described by Hildebrand and Cable (1938). Balbontin and Perez (1979) described the eggs and larvae of a Chilean species, *H. sordidus*.

Although the species of *Hypsoblennius* are shallow-water demersal spawners, their larvae occur routinely in nearshore CalCOFI plankton collections, both in oblique and surface tows. Larvae of *Hypsoblennius* species are similar in morphology and pigmentation, and identifying them in ichthyoplankton samples has been an intractable problem. Developmental series obtained from eggs of captive adults have been useful in establishing characters for identification of larvae in other fishes. The purpose of this paper is to describe the larvae of *H. jenkinsi* obtained from egg masses of that species and to make comparisons with reared larvae of *H. gentilis*. Information on the reproductive biology of *H. jenkinsi* is also presented.

MATERIALS AND METHODS

Egg masses of *H. jenkinsi* and *H. gentilis* were collected by a diver in Mission Bay, San Diego, and reared in the experimental aquarium at the Southwest Fisheries Center, La Jolla. Brooding males were captured with each egg mass and preserved as voucher specimens after hatching was completed. In all egg collections, the nest was on the inner surface of the shell of the scallop *Hinnites multirugosus*. The shell and brooding male were placed in a plastic bag, taken to the laboratory, and submerged in a 20-liter bucket of filtered seawater. The bag was removed; an airstone was introduced; and the nest was left undisturbed until hatching began. As larvae emerged, they were dipped out with a 1-liter beaker and placed in 100- or 400-liter black fiberglass rearing tanks containing filtered seawater held in water tables at ambient seawater temperatures.

Initially the larvae were fed the rotifer *Brachionus plicatilus,* maintained at a concentration of 50/ml. A liter of a dense algal culture *(Tetraselmnis suesica)* was added daily as food for the *Brachionus*. When the larvae were 10-15 days old, *Artemia* nauplii were

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added at a concentration of about 1 nauplius/ml. Large larvae, juveniles, and adults were fed frozen adult *Artemia,* supplemented with wild zooplankton when available.

Larvae were sampled regularly and preserved in 4 percent Formalin. Some were photographed before preservation to record xanthic pigmentation. Morphometric measurements were made according to the methods described in Sumida et al. (1979), except for the following measurements:

> Greatest body depth = body depth at the cleithral junction.
>
> Pectoral fin length = horizontal distance from the edge of the fin base to the posteriormost margin of the fin blade.
>
> Length of the longest preopercular spine = distance from the base of the spine to its tip.
>
> Snout length = horizontal distance from the anterior edge of head to the edge of the eye.

Meristic counts were taken from specimens cleared and stained using the alcian cartilage staining method of Dingerkus and Uhler (1977) and the trypsin-alizarin red technique of Taylor (1967).

Diameters of field-collected and aquarium-spawned eggs were measured with the ocular micrometer of a stereoscopic microscope. The number of eggs in aquarium spawnings was estimated by counting all eggs in a sample area estimated to be 10 percent of the total egg patch.

The growth curve for *H. jenkinsi* was computed from lengths of Formalin-preserved reared larvae, juveniles, and adults fitted to the Gompertz curve, using a canned program, PAR of BMDP-80 (Dixon and Brown 1979). Pooled lengths were used for larvae less than 40 days old.

Distribution data were taken from fish larvae identification records of CalCOFI collections from 1950 through 1972.

REARING CHRONOLOGY

The first collection of *H. jenkinsi* eggs was made on July 22, 1977. Both valves of the *Hinnites* shell were covered with eggs, estimated to number over 10,000 on one valve. The male measured 73 mm SL. Incubation temperatures ranged from 20.0° to 21.5°C. Subsequent examinations of the shell indicated that about 20 percent of the eggs hatched. The oldest survivors died on day 62, with the largest juvenile reaching 14.1 mm SL.

The second brood was obtained on July 14, 1978. The male measured 44 mm SL. Hatching began on July 16 and lasted for 4 days. Water temperature during incubation and rearing ranged from 19.0° to 23.0°C. Transformation to benthic juveniles was observed on day 53, when larvae had reached 10-13 mm SL. Shells, sponges, and concrete blocks were placed in the rearing tank to provide cover. On day 103 one male and three females, all of about equal size, remained; one, anesthetized with quinaldine, measured 32.0 mm SL.

On day 141 after hatching, a patch of about 450 eggs appeared on the bottom and sides of the rearing tank, covering an area of about 20-25 cm^2. The male fanned the eggs intermittently. A small section of the egg patch was excised from the side of the tank with a scalpel and incubated in a 10-liter pot. Incubation temperatures ranged from 15.2° to 18.0°C. Larvae began to hatch from the eggs after 22 days of incubation (day 163 for the adults). *Brachionus* was added to the rearing pot, but all larvae died within 3 days. On day 240 the male died and was replaced by a field-caught male. Spawning occurred 6 more times, on days 260, 264, 277, 281, 313, and 317 and resulted in clutches of 300-650 eggs, but none of the eggs survived to the hatching stage. The temperatures ranged from 16.0°-19.0°C. The three females died on days 296, 319, and 320 at lengths of 55, 65, and 64 mm SL.

The single egg mass of *H. gentilis* was collected in a *Hinnites* shell on August 9, 1977, along with an 86-mm SL brooding male. Hatching began on August 17 and continued to August 18. Water temperature during incubations was approximately 18.5°C. Larvae fed on *Brachionus* but suffered a high mortality; the last ones died 21 days after initial hatching at lengths of 6.7 mm SL.

DESCRIPTION OF DEVELOPMENTAL STAGES

Eggs

Wild eggs of *H. jenkinsi* reported on here are deposited in a single layer on *Hinnites* valves. They are slightly flattened in the plane of the substrate and are attached by an adhesive disc. The yolk is granular, and the perivitelline space is narrow. Diameters of 29 field-collected eggs from two broods ranged from 0.69 to 0.80 mm ($\bar{x}$ = 0.75 ± 0.029 SD). Diameters of 22 aquarium-spawned eggs from two masses ranged from 0.71 to 0.78 mm ($\bar{x}$ = 0.75 ± 0.023 SD). The aquarium-spawned eggs were used in the following description.

A striking feature of *H. jenkinsi* eggs is the presence of a clump of violet inclusion bodies and a clump of golden yellow oil globules within the yolk. As reported for the eggs of *H. hentzi* (Hildebrand and Cable 1938), the violet bodies disperse, shrink, and fade with development. They disappear before hatching. The oil globules have a similar fate, although some may persist in newly hatched larvae. After about 3 days of development the outline of the embryo is clearly visible in an equatorial position. After 7 days the embryo extends about two-thirds of the way around the yolk, and the heart is beating. The body axis is now located on the side of the yolk mass facing the substrate, and the head faces upward. By day 17 the body begins to twitch, and by day 19 the eyes are rotating. Hatching occurs at the end of the third week.

The first pigment to develop in the embryo is a covering of scattered melanophores over the upper and lower surfaces of the yolk mass. At the end of the first week the eyes begin to develop melanistic pigment. Midway through embryonic development, melanophores begin to form along the dorsal surface of the gut and on the medial surfaces of the pectoral fin buds. During the third week of the development melanophores appear at the bases of the otic capsules, and a medial series extends along the base of the cranium to the snout. Melanophores cover the medial surface of each pectoral fin. One or two melanophores are present on the ventral surface of the gut just anterior to the anus. A ventral midline series of small, evenly spaced melanophores extends from the anus to the posterior region of the tail. Melanophores are absent on the remaining yolk mass.

Larvae

Morphology. Development of *H. jenkinsi* larvae is illustrated in Figure 1. Body measurements of *H. jenkinsi* and *H. gentilis* are listed in Tables 1 and 2, and proportions are summarized in Table 3. Both species hatch at about 2.5 mm, with large heads, thin tapering bodies, and prominent functional pectoral fins. Both species are similar to the larvae of other species of the genus (Hildebrand and Cable 1938; Balbontin and Perez 1979). Snout-anus length and pectoral fin length are slightly greater in larvae of *H. jenkinsi* than in *H. gentilis*. In *H. jenkinsi*, three major preopercular spines develop, the upper two approximately equal in length (Figure 2). The middle spine is 15 percent of the head length in a 7.6-mm larva and undergoes a reduction to 3 percent of head length at 17.9 mm ($\bar{x} = 9.1 \pm 4.15$ SD for the series). Preopercular spines are absent in *H. jenkinsi* specimens larger than 18.0 mm SL.

TABLE 1
Average Measurements (mm) of Reared Larvae of *Hypsoblennius jenkinsi*

Body length	N	Range	Snout length	Head length	Snout to anus	Eye width	Greatest body depth	Pectoral fin length	Length of longest preopercular spine	Length of cirrus
2.5	1	-	.10	.56	.98	.28	.56	.28	<.02	
2.8	7	2.76- 2.82	.11	.61	1.0	.29	.62	.37	.02	
2.9	7	2.8 - 3.0	.12	.64	1.1	.28	.59	.39	.05	
3.2	6	3.0 - 3.4	.14	.67	1.2	.31	.64	.46	.04	
3.6	5	3.5 - 3.8	.15	.74	1.4	.34	.73	.48	.08	
4.5	6	4.0 - 4.6	.19	1.0	1.6	.44	.92	.82	.06	
4.7	7	4.7 - 4.8	.21	1.1	1.8	.47	.98	.92	.09	
4.9	6	4.9 - 5.0	.23	1.2	2.0	.51	1.1	1.1	.13	
5.2	12	5.0 - 5.2	.21	1.2	2.1	.52	1.1	1.2	.16	
5.7	7	5.3 - 6.3	.25	1.5	2.4	.66	1.3	1.5	.19	
5.8	5	5.6 - 6.0	.22	1.5	2.6	.74	1.4	1.7	.22	
6.2	5	6.1 - 6.6	.23	1.6	2.7	.75	1.6	1.8	.27	
7.6	3	7.2 - 7.9	.20	2.1	3.3	.92	2.1	2.3	.31	
8.9	3	8.6 - 9.6	.30	2.6	4.0	1.1	2.3	2.8	.32	
10.5	4	10.2 -10.8	.38	2.9	4.6	1.2	2.6	3.1	.38	.04
11.3	1		.30	3.1	4.6	1.3	2.6	2.8	.28	.35
12.6	1		.56	3.2	5.5	1.3	3.2	3.7	.48	.12
12.8	1		.40	3.7	5.8	1.5	3.3	4.1	.32	.43
14.1	1		.52	3.8	6.6	1.8	3.8	4.6	.24	.22
15.7	1		.68	4.9	7.3	1.7	4.2	5.1	.20	.69
16.8	1		.75	4.8	7.8	1.7	4.1	4.9	.25	.30
17.9	1		.80	4.8	8.1	1.8	4.8	5.8	.16	.56
18.2	1		.73	5.3	8.5	1.8	5.2	5.7	—	.72
18.6	1		.65	5.3	8.6	1.8	4.9	5.6	—	.52
19.7	1		.89	5.3	9.5	1.9	5.0	6.1	—	.80

Specimens larger than 11 mm are considered early juveniles.
Specimens between dashed lines are undergoing notochord flexion.

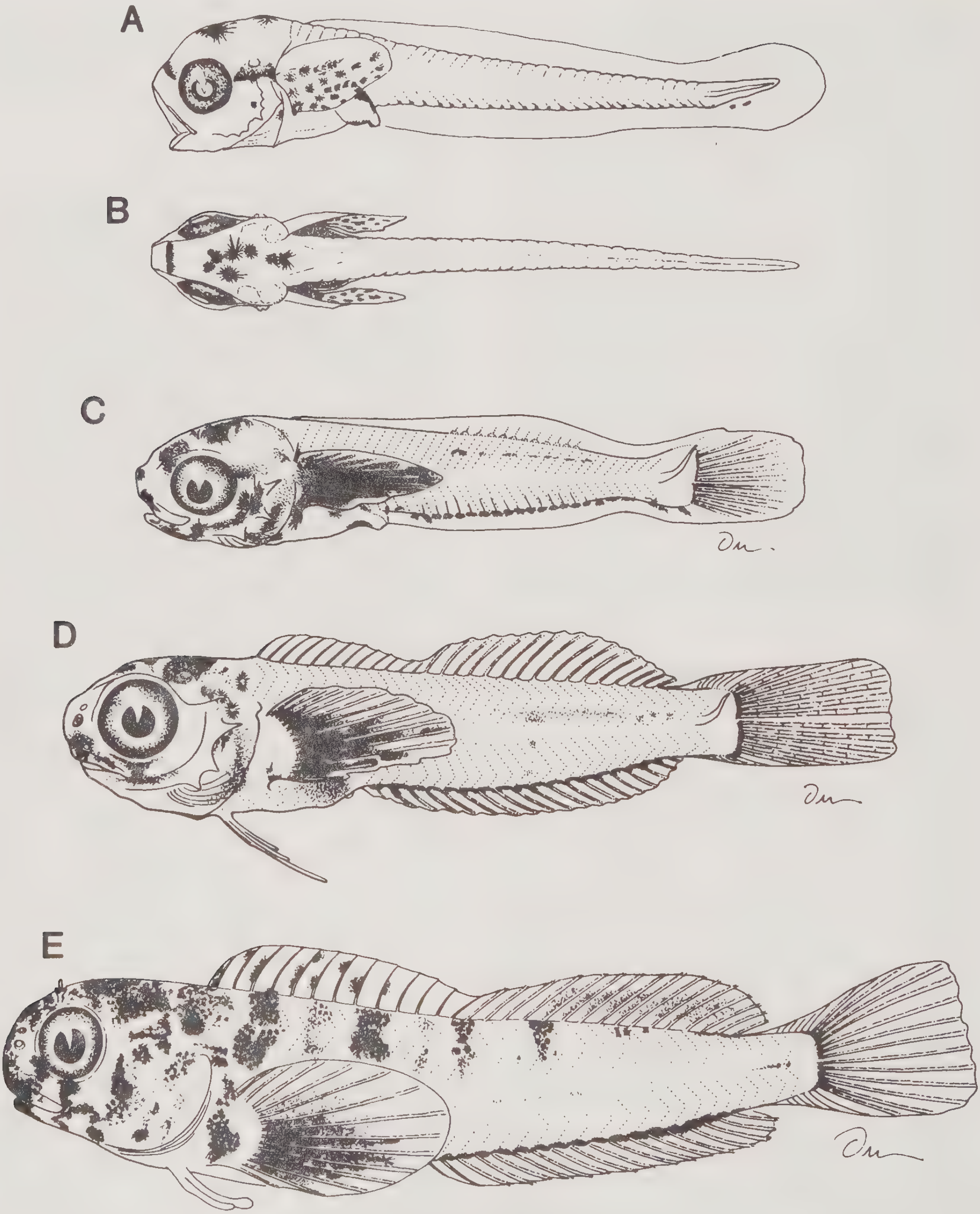

Figure 1. Reared specimens of *Hypsoblennius jenkinsi: A.* 4.3-mm larva (day 7); *B.* 4.3-mm larva, dorsal view; *C.* 5.3-mm larva; (day 29); *D.* 10.2-mm larva (day 34); *E.* 18.6-mm juvenile (day 58).

TABLE 2

Average Measurements (mm) of Larvae of *Hypsoblennius gentilis*

Body length	N	Range	Snout length	Head length	Snout to anus	Eye width	Greatest body depth	Pectoral fin length	Length of longest preopercular spine	Length of cirrus
2.5	7	2.4-2.6	.10	.52	.92	.25	.50	.33	—	
2.7	4	2.6-2.8	.12	.57	.96	.28	.55	.36	.02	
3.1	1		.12	.62	1.1	.28	.60	.46	.02	
3.5	4	3.4-3.6	.15	.77	1.4	.34	.76	.53	.08	
3.7	4	3.6-3.7	.20	.84	1.4	.35	.84	.58	.08	
3.9	5	3.8-3.9	.18	.90	1.5	.38	.80	.70	08	
4.1	1		.20	.94	1.5	.36	.86	.90	.06	
4.4	3	4.4	.19	1.0	1.6	.40	.93	.89	.09	
4.6	3	4.6-4.7	.21	1.1	1.8	.45	.87	.96	.12	
4.8	4	4.8	.20	1.1	1.9	.44	1.0	1.1	.12	
6.7	1		.28	1.9	2.9	.80	1.6	2.0	.20	

Specimens between dashed lines are undergoing notochord flexion.

TABLE 3

Comparative Morphometry of *H. jenkinsi* and *H. gentilis*

Body proportion	*H. jenkinsi*	*H. gentilis*
Snout-anus/body length		
A	37.4 ± 1.2 (33-40)	36.1 ± 1.3 (34-38)
B	40.4 ± 2.3 (35-47)	38.8 ± 1.9 (37-43)
C	44.1 ± 1.8 (42-49)	
D	45.6 ± 2.1 (41-48)	
Snout length/body length		
A	4.2 ± 0.6 (3-5)	4.2 ± 0.7 (3-6)
B	4.4 ± 0.6 (3-5)	4.6 ± 0.7 (4-6)
C	3.5 ± 0.7 (3-5)	
D	3.7 ± 0.7 (3-5)	
Head length/body length		
A	21.5 ± 1.2 (19-23)	21.0 ± 1.0 (19-22)
B	23.5 ± 1.8 (20-28)	23.0 ± 1.6 (18-27)
C	27.2 ± 2.2 (23-31)	
D	27.9 ± 1.8 (25-31)	
Eye diameter/body length		
A	9.8 ± 0.6 (9-11)	10.1 ± 0.6 (9-11)
B	10.2 ± 0.8 (9-12)	9.5 ± 0.6 (9-11)
C	12 4 ± 0.8 (11-14)	
D	10.6 ± 1.0 (10-13)	
Greatest body depth/body length		
A	20.7 ± 1.4 (19-24)	20.1 ± 1.0 (18-24)
B	21.6 ± 1.7 (19-26)	21.2 ± 1.9 (18-24)
C	25.5 ± 1.4 (23-30)	
D	25.8 ± 1.7 (23-29)	
Pectoral fin length/body length		
A	12.9 ± 2.9 (11-17)	13.4 ± 1.4 (11-16)
B	22.4 ± 4.0 (16-30)	18.8 ± 3.3 (14-25)
C	29.5 ± 2.0 (26-33)	
D	30.5 ± 2.3 (25-33)	
Longest preopercular spine/head length		
A	7.2 ± 3.9 (3-14)	2.8 ± 1.3 (1-5)
B	10.1 ± 3.9 (1-19)	10.1 ± 2.8 (6-15)
C	16.1 ± 2.4 (13-20)	
D	6.9 ± 5.7 (0-19)	
Cirrus length/head length		
C	2.4 ± 0.7 (2-3)	
D	10.3 ± 3.8 (3-15)	

A = preflexion, B = flexion, C = postflexion, D = juvenile (specimens > 11.0 mm). Values are mean, standard deviation, and range of percentage of body length or head length.

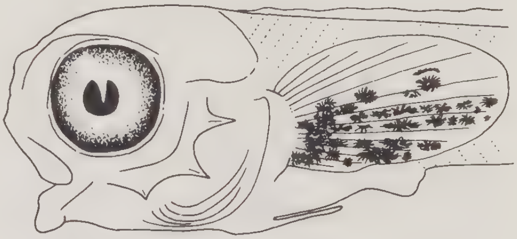

Figure 2. Preopercular spination of *Hypsoblennius jenkinsi* larva, 7.6 mm.

Fin formation. Pectoral fin rays begin to ossify at about 4.0 mm body length in both species, and the adult complements (12-15 for *H. jenkinsi;* 11-12 for *H. gentilis*) are formed during caudal fin flexion (Table 4). Principal caudal fin rays begin ossifying at about 4.0 mm in both species, and the adult complement of 7 superior and 6 inferior rays is present at the completion of notochord flexion. Dorsal, anal, and pelvic fin anlagen appear during caudal fin flexion, and the adult complements are present between 8.0 and 9.0 mm in *H. jenkinsi*.

Pigmentation. Newly hatched *H. jenkinsi* and *H. gentilis* larvae have four areas of melanstic pigmentation: the dorsal surface of the gut, with one or two preanal melanophores along the ventral midline; the medial surfaces of the pectoral fin base and blade; along the base of the cranium from the otic capsules to the snout; and along the ventral midline, with a series of melanophores extending posteriorly from just behind the anus to the tip of the notochord. In *H. jenkinsi* the number of principal postanal ventral midline melanophores ranges from 21-27 ($\bar{x}$= 23.6 ± 1.3 SD for 26 specimens counted). In *H. gentilis* the range was 22-26 ($\bar{x}$ = 24.1 ± 1.2 SD for 23 specimens).

TABLE 4

Meristic Characters of Cleared and Stained Larvae of *H. jenkinsi* and *H. gentilis*

Body length	Source	Vertebrae	Principal caudal rays	Procurrent caudal rays	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin
H. jenkinsi								
4.0	reared	35	5 + 6				12, 12	
4.4	"	10 + 24	5 + 3				11, 11	anlagen
5.0	"	35	5 + 6	0 + 2	12	16	12, 13	anlagen
5.7	"	10 + 24	7 + 6	1 + 2	12	15	13, 13	1, 1
6.1	"	10 + 25	7 + 6	1 + 3	14	17	13, 13	1, 1
7.3	"	10 + 24	7 + 6	5 + 5	XII, 15	I, 17	14, 14	4, 4
8.4	"	10 + 24	7 + 6	7 + 7	XIII, 16	II, 17	12, 12	I,3;I,3
9.8	"	10 + 24	7 + 6	7 + 8	XII, 17	II, 17	13, 13	I,3;I,3
10.3	"	10 + 24	7 + 6	7 + 7	XII, 16	II, 18	14, 14	I,3;I,3
12.1	"	10 + 24	7 + 6	8 + 8	XII, 15	II, 17	13, 13	I,3;I,3
17.1	"	10 + 24	7 + 6	7 + 6	XII, 15	II, 17	14, 14	I,3;I,3
H. gentilis								
3.7	reared	35						
4.1	"	35	2 + 2				11, 11	
4.6	"	10 + 25	4 + 4				9, 9	
4.8	"	10 + 25	4 + 4				11, 11	

Specimens between dashed lines are undergoing flexion.

There are 3-5 small, irregularly spaced melanophores at the tip of the tail.

In both species pigmentation increases during larval development primarily on the head, above the brain, on the nape, snout, jaws, operculum, and isthmus. Pigment descends laterally on the gut wall. During flexion, the irregular group of melanophores at the end of the notochord develops into a line of pigment on the posterior margin of the hypural plates. In postflexion *H. jenkinsi* the pectoral fin blade and median surface of the base remain heavily pigmented except for the dorsal region of the blade, which is unpigmented. *H. jenkinsi* above 18 mm SL develop melanophores on the lateral surface of the pectoral base. In early postflexion larvae of *H. jenkinsi* a series of melanophores develops on the dorsal surface of the vertebral column. At 10-11 mm SL, external dorsal pigment begins to develop. Pigment is arranged in a series of 5 to 7 saddles, beginning at the nape and eventually extending to the middle of the soft dorsal fin, with scattered melanophores on the dorsal margin posterior to the saddles. The saddles extend downward about one-fourth of the body depth. Paler saddles develop between the darker saddles. Concurrent with the dorsal pigment expansion a row of melanophores develops along the lateral line, beginning posterior to the pectoral fin and gradually extending to the tail.

Growth rate. The incubation time for *H. jenkinsi* eggs was determined from the laboratory-spawned egg mass, which began to hatch on day 21 and continued for about 2 days. During the 23-day period temperatures in the rearing tank ranged from 15.2-18.0°C. Hildebrand and Cable (1938) observed hatching of *H. hentzi* in 10-12 days at 24-27°C, and Hubbs (1965) recorded incubation times for *H. jenkinsi* of 14-21 days at 15-18°C and 6-8 days at 24-27°C in temperature-controlled experiments. In the field, eggs in one nest are deposited by several females over a period of time, and consequently hatching occurs over several days (Losey 1968).

The growth rate of the *H. jenkinsi* larvae was computed from lengths of 960 individuals in the two reared groups, fitted to the generalized Gompertz growth curve

$$Y_t = Y_o e^{\frac{\alpha}{\beta}(1-e^{-\beta t})}$$

where t = time in days, y = length in millimeters, α = the instantaneous rate of growth at age 0, and β is the change in growth rate. The resultant growth rate, $Y_t = 1.2845\ e^{3.92(1-e^{-.0177t})}$, is plotted in Figure 3. Sexual maturity, as shown by the laboratory spawning, occurs in the region of the upper break in the curve, at about 40-50 mm SL and 150 days of age. The length reached in 320 days by reared specimens, 60-65 mm, and the maximum length of *H. jenkinsi* reported by Stephens et al. (1970) as 89 mm, indicates that this species approaches its maximum length by the end of its first year.

DISTRIBUTION

Hypsoblennius larvae are not taken in great numbers but are collected over a wide latitudinal range, from CalCOFI line 73, just north of Pt. Arguello, California, to CalCOFI line 150, south of Magdelena Bay, Baja California Sur. They have also been taken in

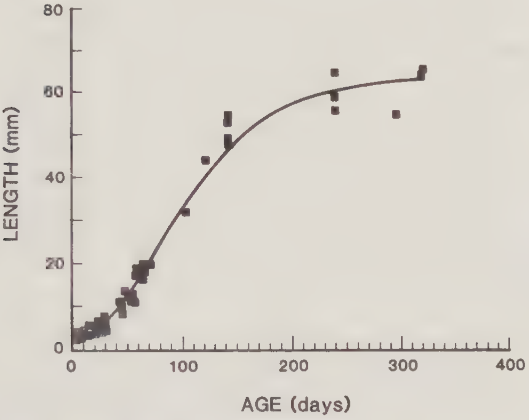

Figure 3. Growth curve for reared *Hypsoblennius jenkinsi*.

oblique tows in the Gulf of California. During October 1972 on CalCOFI Cruise 7210, when surface as well as oblique collections were made over an extended CalCOFI pattern, *Hypsoblennius* larvae were captured in greater numbers at the surface. *Hypsoblennius* larvae usually were collected close to shore but occasionally were taken well offshore, as at stations 107.70 and 133.70. The 781 occurrences of *Hypsoblennius* larvae in CalCOFI oblique tows from 1950–72 and the 13 occurrences in neuston stations in 1972 are plotted in Figure 4 and summarized in Table 5.

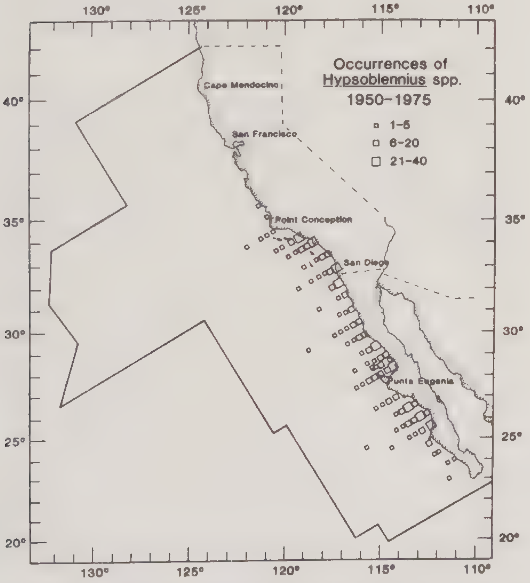

Figure 4. Occurrences of *Hypsoblennius* spp. larvae in CalCOFI plankton collections. Standard CalCOFI sampling pattern bounded by solid line.

TABLE 5

Areal and Seasonal Occurrences of *Hypsoblennius* ssp. Larvae in CalCOFI Collections

Area	% Occurrences	Month	% Occurrences
Lines 60- 77	0.3%	Jan.-Mar.	6.9%
80- 97	30.3	Apr.-June	12.4
100-119	22.2	July-Sept.	54.2
120-137	45.0	Oct.-Dec.	26.5
140-157	2.2		

Values are percent of total occurrences.

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USE OF M50-50 AS A THERAPEUTIC DRUG FOR M99-INDUCED TRAUMA

MITCHELL K. TAYLOR, Department of Ecology, University of Minnesota, Minneapolis, MN 55455; DOUGLAS P. DEMASTER, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038; SALLIE P. SHELDON, Department of Ecology, University of Minnesota, Minneapolis, MN 55455; and FRED E. SORENSEN, National Fish and Wildlife Laboratory, 4454 Business Park Boulevard, Anchorage AK 99503.

The recent decision of the U.S. Federal Drug Administration placing Sernylan (phencyclidine) on the list of Schedule 2 drugs has caused its previous manufacturers to cease production. M99 (etorphine) is also a Schedule 2 drug, but is still available. M99 has been used successfully to immobilize wild and captive bears for many years (Flyger et al., Trans. North Am. Wildl. and Nat. Resour. Conf. 32:107–119, 1967; Alford et al., J. Am. Vet. Med. Assoc. 164:702–705, 1974; Patenaude, J. Am. Vet. Med. Assoc. 175:1006–1007, 1979). One of the problems with the use of M99 is that it acts as a central nervous system depressant and may reduce respiration rates to dangerously low levels. Here we report an attempt to increase respiration by administration of a partial recovery dose of the antagonist M50-50 (diprenorphine).

After a brief chase, a 193-kg young adult male polar bear (*Ursus maritimus*) was given 4.5 mg of M99 intramuscularly via a "Cap-Chur" syringe dart (Palmer Chem. Co., Douglasville, Ga.). The bear was immobile 12 minutes after the injection, and was approached 8 minutes later. Approximately 30 minutes after injection, the respiratory rate had diminished to 1 breath/minute. Because 2 mg of M50-50 are required to reverse the effects of 1 mg of M99, 1 mg of the antagonist (approximately 11% of the recovery dose) was administered intramuscularly to try to increase the respiration rate. About 15 minutes later respiration was still around 1 breath/minute, and an additional 1 mg of M50-50 was given.

Respiration improved visibly a few minutes after the 2nd injection. Six minutes later, the bear suddenly lifted its head, rose to a crouch, then lay back down with its head between its paws. As we approached the bear to administer additional M99, it suddenly arose and ran off.

Use of M50-50 as a drug to combat M99-induced trauma, specifically respiration depression, is not recommended unless rapid and complete recovery is desired.

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An acoustic technique for determining diurnal activities in leopard (*Hydrurga leptonyx*) and crabeater (*Lobodon carcinophagus*) seal

J. A. Thomas

Hubbs Sea World Research Institute, 1700 South Shores Road, San Diego, CA, U.S.A. 92109

AND

D. P. DeMaster

National Marine Fisheries Service, Southwest Fisheries Center,
P.O. Box 271, La Jolla, CA, U.S.A. 92038

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Hourly variations in the rate of underwater vocalizations produced by leopard (*Hydrurga leptonyx*) and crabeater seals (*Lobodon carcinophagus*) were compared with counts of these seals on ice floes. For both species maximum "haulout" corresponded with minimum underwater vocalizations. Consequently, sampling the vocal behaviour of pinnipeds may be used to determine their diurnal haulout pattern. This underwater vocalization rate potentially may be used to calculate a series of hourly correction factors that compensate for submerged seals not seen during a census.

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Les variations horaires du taux des cris sous l'eau de léopards de mer (*Hydrurga leptonyx*) et de phoques crabiers (*Lobodon carcinophagus*) ont été comparés au nombre de phoques sur les glaces flottantes. Chez les deux espèces, les périodes où le plus grand nombre de phoques sont hors de l'eau correspondent aux périodes où les cris sont le moins fréquents. Il est donc possible de déterminer les patterns de sortie de l'eau des pinnipèdes en échantillonnant leur comportement vocal. Il est permis de croire aussi que le taux des cris sous l'eau pourra éventuellement servir à calculer une série de facteurs de correction horaires destinés à compenser l'absence des phoques en plongée au moment d'un recensement.

[Traduit par le journal]

Introduction

Ship-based surveys of Antarctic seals during the austral summer have shown that leopard (*Hydrurga leptonyx*), Weddell (*Leptonychotes weddelli*), crabeater (*Lobodon carcinophagus*), and Ross (*Ommatophoca rossi*) seals exhibit predictable hourly variations in "haulout" (Gilbert and Erickson 1977). Many population studies have incorporated a correction factor that compensates for hourly count differences (Siniff et al. 1971; Gilbert and Erickson 1977). Radio telemetry techniques are valuable for determining the diurnal haulout of Weddell seals in fast ice regions (Siniff et al. 1971); however, such techniques are not applicable in pack ice because of the mobility of the haulout platform.

Currently, two techniques are used to determine the haulout pattern of pinnipeds: hourly counts of animals and radio tracking of movements in and out of the water. These techniques require continuous long-term contact with the animals. Hourly counts of animals that are hauled out in inaccessible areas may not be possible. Weather, limited daylight, and cost make 24-h counts unrealistic. Radio telemetry techniques have limited application in unstable habitats, such as pack ice, where both the animals and the haulout platforms are moving. Transmitter attachment and receiver durability often are problems in the field. To surmount these problems we developed an alternative technique, a passive acoustic recording system that automatically monitors pinniped vocal activities even in remote areas.

Stirling and Siniff (1979) documented four underwater vocalizations from the leopard seal (*Hydrurga leptonyx*) and one from the crabeater seal (*Lobodon carcinophagus*). Both species vocalize frequently during the breeding season. The object of our study was to determine if the diurnal pattern of underwater vocalizations is negatively correlated with the haulout pattern for these two pack-ice species. If so, it is possible theoretically to calculate a series of correction factors that compensate for submerged seals during a given hour of a census.

Materials and methods

Using the RV *Hero* as a survey platform, we counted seals along the Antarctic Peninsula (Martel and Ezcurra Inlets, Bransfield and Gerlache Straits, and Bismarck and Dallmann Bays) from 26 October to 21 November 1978. All leopard and crabeater seals seen on ice floes within 400 m of the ship were

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counted in a continuous census during daylight hours (0400 to 2200). For each sighting the sex, age, and species of seal and the location, time, and amount of ice cover were noted. From these data we calculated the mean number of seals on the ice for each hour.

Underwater vocalizations were recorded automatically with an Interoceans R130 hydrophone (frequency response, 0.03–10.00 kHz ± 1.0 db) and a Superscope C101A cassette recorder (frequency response, 0.20–5.0 kHz) controlled with a digital timer. This system was placed on an ice floe in an insulated box heated with thermal packs; it sampled underwater vocalizations for 2.5 min every hour. A radio-frequency transmitter on the ice floe and a ship-based receiver were used to relocate the system 24 h later. Crabeater and leopard seal vocalizations were recorded in Martel Inlet on 28–31 October, in Bismarck Bay on 2–5 November, in Dallmann Bay on 7–14 November, and in Ezcurra Inlet on 18 November 1978 ($n = 17$ days sampled).

In the laboratory the number of audible and identifiable underwater vocalizations per sample was tallied for each species. Calls were identified to species by referring to sound spectrograms in Fig. 1 of Stirling and Siniff (1979). The radial distance of sound reception using this system was not measured, but because the automatic gain control in the cassette recorder was used and oceanographic conditions were similar we assume that the same area was sampled during each recording. Seals vocalizing near the hydrophone could saturate the recording and block distant vocalizations; thus, vocalization rates may have been higher. The age and sex composition of the seals producing vocalizations could not be controlled; however, the majority of animals observed during our survey were adults.

Results and discussion

A one way analysis of variance (ANOVA), using the number of leopard seals on the ice as the random variable and each hour from 0400 to 2200 as a treatment, showed significant heterogeneity ($F_{0.05} = 1.97$, critical value = 1.66). Maximum leopard seal haulout occurred between 0900 and 1800 and minimum haulout between 1900 and 2200, and 0400–0800 (Fig. 1*a*). Hourly differences in crabeater seal counts showed similar variations ($F_{0.05} = 2.62$, critical value = 1.66). Maximum haulout was from 0900 to 1900 and minimum was from 2000 to 2200 and 0400 to 0800 (Fig. 2*a*). For both species, the period from 2300 to 0300 could not be sampled because of darkness, but seals are believed to be in the water during this period.

Hourly differences in underwater vocalization rates were compared using a one-way ANOVA with the vocalization rate per minute as the random variable and each of 24 h as a treatment. Significant differences were found for leopard ($F_{0.05} = 3.34$, critical value = 1.59) and crabeater ($F_{0.05} = 2.05$, critical value = 1.59) seals. For both species the peak period for underwater vocalizations was between 1900 and 0600, whereas the minimum underwater vocalization rate occurred between 0900 through 1800 (Figs. 1*b* and 2*b*).

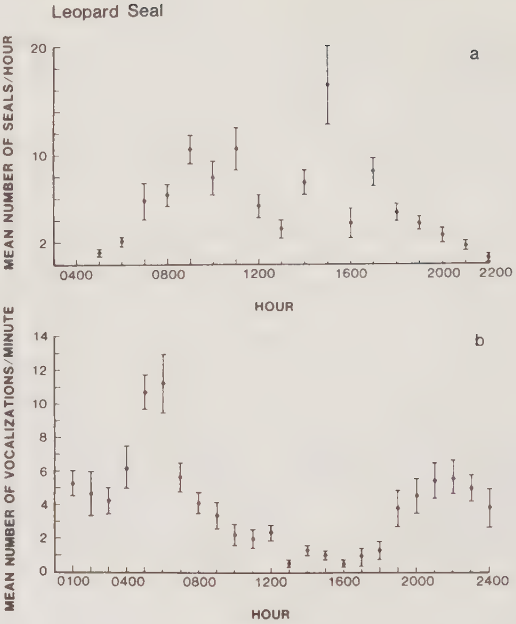

FIG. 1. (*a*) Mean (and 95% confidence interval) number of leopard seals hauled out per hour for each hour of observation. (*b*) Mean (and 95% confidence interval) number of underwater vocalizations per minute for each hour.

There is a significant negative correlation ($p < 0.01$) between the mean underwater vocalization rate per minute and the mean number of seals counted per hour (leopard seal, $r = -0.55$ and crabeater seal, $r = -0.66$).

Both crabeater and leopard seals produced pups during our study period. Crabeater seals were seen as male–female pairs on floes, and Siniff et al. (1979) indicated that courtship and mating occur during this period. The mating season of leopard seals is not well known; Harrison et al. (1968) suggested that there is no delayed implantation as in other antarctic seals and that mating occurs around late December or January. However, Sinha and Erickson (1972) suggested that delayed implantation occurs in leopard seals and mating is in November as in other antarctic phocids. The stage of the reproductive cycle affects vocal activity; both crabeater and leopard seals were vociferous during our study and recordings in January and February near the Antarctic Peninsula show a dramatic decrease in vocalizations by these seals (Thomas et al. 1981).

There are technical problems associated with accurately monitoring the haulout pattern of pinnipeds. Remote haulout sites, such as pack ice, offshore rocks,

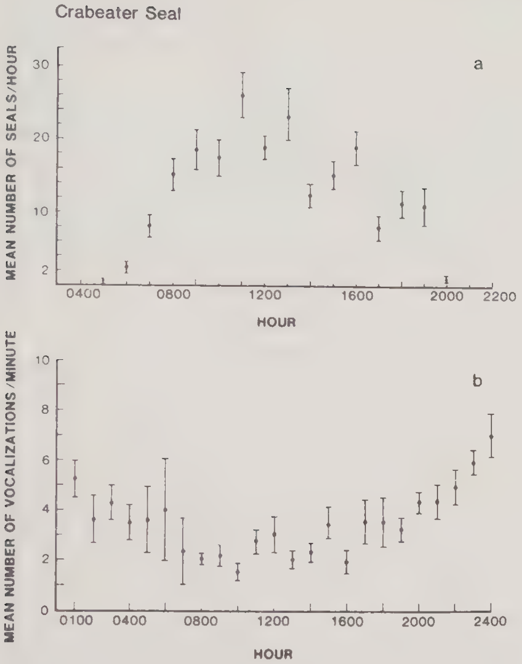

FIG. 2. (*a*) Mean (and 95% confidence interval) number of crabeater seals hauled out per hour for each hour of observation. (*b*) Mean (and 95% confidence interval) number of underwater vocalizations per minute for each hour.

or inaccessible beaches, often preclude observations of haulout. Observer or survey vessel disturbances often disrupt haulout behavior. The proposed technique offers an alternative method to investigate hauling activity in pinnipeds. Underwater vocalizations are negatively correlated with the diurnal haulout of leopard and crabeater seals and our acoustic sampling system may have practical application for a wide variety of pinnipeds and haulout sites. Several pinnipeds are vocal under water: *Odobenus rosmarus* (Schevill et al. 1966); *Phoca hispida* (Stirling 1973); *Pagophilus groenlandicus* (Møhl et al. 1975); *Erignathus barbatus* (Ray et al. 1969); and *Leptonychotes weddelli* (Thomas 1979). Some pinnipeds are more vocal while hauled out, e.g., *Zalophus californianus* (Bartholomew and Peterson 1967), *Mirounga angustirostris* (Bartholomew and Collias 1962), and some species of fur seals, *Arctocephalus* (Stirling and Warneke 1971). This acoustic system can be modified for either underwater or airborne sampling. Diurnal haulout may change seasonally or between haulout sites and monitoring vocalization rates may provide a technique for documenting these changes.

In summary, using the hourly rate of underwater or airborne vocalizations may be a practical technique to document the diurnal haulout pattern of pinnipeds. Its application in remote haulout sites and its noninterfering mode of operation are advantages. This technique can be used for determining the diurnal haulout pattern of many pinnipeds. A series of census correction factors can be calculated using hourly vocalization rates; however, we recommend sampling in the same area and season as the census because the density of seals may vary between areas, vocalizations may decrease outside the breeding season, and high densities may induce contageous vocalizing.

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ANALYSIS OF DOUBLE-TAGGING EXPERIMENTS

JERRY A. WETHERALL[1]

ABSTRACT

Statistics arising from double-tagging experiments may be applied to estimate tag-shedding probabilities directly, to estimate parameters of underlying theoretical shedding models, or to estimate mortality rates free of tag-shedding bias.

Simple maximum likelihood estimators of tag retention rates, along with their asymptotic variances, may be derived assuming conditional multinomial sampling models. If specific models of shedding are of interest, limitations of existing theory may be reduced by assuming the Type II shedding rate is time-dependent. In the more realistic models and their simpler precursors, parameters may be estimated by least squares or by maximum likelihood methods. Complications arising in the direct maximization of the conditional likelihood may be circumvented by use of iteratively reweighted Gauss-Newton algorithms available in standard statistical software packages. Simple diagnostic plots may be helpful in model selection.

When a sequence of double-tagged cohorts is released, recapture statistics may be treated separately or combined to estimate common shedding rates, but a more general linear model may be used to fully exploit the structure of the experiment and to estimate both common parameters and those unique to each cohort.

When recapture times are unknown but the experiment spans a sufficiently long period, the ratio of constant Type II tag-shedding rate to constant Type II total mortality rate may be estimated. Under similar circumstances, but with exact recapture times known for each fish, maximum likelihood estimates of both parameters may be computed

If only the Type II mortality rate is of interest, it may be estimated free of tag-shedding bias by simple linear regression of appropriate double-tagging statistics, if Type II shedding and Type II mortality are constant during the experiment.

The estimation of fishing mortality rate, exploitation rate, and population size through mark and recapture experiments is often complicated by the incidental shedding or loss of marks. Failure to account for tag shedding may lead to biased parameter estimates. Thus a well-designed tagging experiment will incorporate some provision for estimating shedding rates and computing correction factors.

The approach usually taken is to release a group, or perhaps several groups of double-tagged fish, and then to estimate shedding rates using information on the number of fish returned in a sequence of recapture samples still bearing both tags and on the number of returns with only one tag remaining. A variety of statistical methods and estimation procedures have been developed. Papers by Beverton and Holt (1957), Gulland (1963), Chapman et al. (1965), Robson and Regier (1966), Chapman (1969), Bayliff and Mobrand (1972), Seber (1973), Laurs et al. (1976), Arnason and Mills (1981), Kirkwood (1981), and Seber and Felton (1981) are particularly noteworthy. In recent years attention has focused primarily on the regression methods developed by Chapman et al. (1965) and extended first by Bayliff and Mobrand (1972) and most recently by Kirkwood (1981).

Despite the extensive literature on double-tagging there is need for an integration of existing thought and for development of new ideas and statistical methods. Accordingly, this paper surveys basic tag-shedding theory and the most widely used analytical techniques, and describes a variety of new models and estimation procedures. Left unaddressed are several important aspects of planning double-tagging experiments. These are the subject of a companion paper by Wetherall and Yong (1981).

TAG LOSS IN SINGLE-TAGGING EXPERIMENTS

To establish a context for later derivations we begin by reviewing the process of tag loss in a population of single-tagged fish. In such a popu-

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

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lation, losses may be caused by fishing mortality or recapture, natural mortality, tagging mortality (mortality induced by the application or presence of the tag), permanent emigration, or by tag shedding. In addition, recaptured tags are considered "lost" if not detected in the catch and recovered, or, when recovered, if not returned or reported.

Beverton and Holt (1957) recognized two kinds of losses, which they designated Type I and Type II (these are called Type A and Type B by Ricker 1975). Type I losses are those which, in effect, reduce the number of tags initially put out. They result from the pulse of tagging mortality and tag shedding occurring immediately after release (or in a relatively brief period following release) and from the nonrecovery and nonreporting of tag recaptures. Type II losses are those happening steadily and gradually over an extended period following release of the tagged fish.

These relations may be stated more succinctly in a simple mathematical model. Let $E(r_i)$ denote the expected number of returns of tags recaptured in the ith time interval following the release of $N_s(0)$ single-tagged fish. Then

$$E(r_i) = \pi\,\rho\,N_s(0) \int_{t_i}^{t_i+\Delta_i} F(u)\,\zeta(u)\,\exp\left(-\int_0^u H(x)\,dx\right)du$$

where
t_i = time at the beginning of interval i
Δ_i = length of time interval i
$1-\pi$ = probability that a tag is lost due to immediate tagging mortality
$1-\rho$ = probability that a tag is shed immediately following release
$F(u)$ = instantaneous fishing mortality rate at time u
$1-\zeta(u)$ = probability that a tag recaptured at time u is not recovered and reported (a Type I loss)
$H(x)$ = total instantaneous rate of Type II tag loss at time x.

Here $H(x)$ represents the unspecified combined effects of fishing mortality, $F(x)$, natural mortality, $M(x)$, instantaneous tag shedding, $L(x)$, and remaining losses, $G(x)$. The usual assumptions are that the Type II losses operate in the manner of independent Poisson processes with constant rates and that the recovery and reporting rates also are constant. Under these conditions the model takes the familiar form

$$E(r_i) = \eta\,N_s(0)\left(\frac{F}{F+X}\right)\Big(1-\exp(-(F+X)\Delta_i)\Big)\Big(\exp(-(F+X)t_i)\Big) \qquad (1)$$

where $\eta = \pi\,\rho\,\zeta$
$X = M + L + G$.

A variety of estimation schemes based on this equation have been developed, notably by Paulik (1963). These have been reviewed along with other mark-and-recapture approaches by Cormack (1968) and Seber (1973). The importance of assumptions on Type I and Type II losses in these procedures depends on which parameters are of central concern in the experiment. In fisheries applications the parameter most often focused on is the fishing mortality rate, F. Paulik's single-release regression model with constant Δ, for estimating F and the exploitation rate, $\mu = (F/(F+M))[1-\exp(-(F+M)\Delta)]$ stems directly from Equation (1). In this situation, if Type I losses are present the model will estimate ηF rather than F. Subsequent estimates of X will be too large. Further, estimates of the exploitation rate will be negatively biased, and if these are used along with $N_s(0)$ to estimate total population sizes, such estimates will be inflated. Of course, this is the general effect of Type I losses on Petersen estimates.

If Type II tagging mortality or Type II tag shedding occur, the estimate of F from this single-release model will not be affected, but the estimate of μ will be less than the true exploitation rate of the unmarked population.

Sometimes all recaptures are made during subintervals of equal length imbedded and irregularly spaced within the total recapture period (e.g., in a salmon fishery with a complex pattern of open and closed periods). In this case, Paulik shows that the single-release model based on Equation (1) will give estimates of F and X

which are unaffected by Type I losses, and in fact will yield an estimate of η as well as the usual estimates of F and X. Since the conditions required for this scheme will not often be encountered, it will usually be necessary to conduct a multiple-release experiment, with at least one preseason release, in order to obtain separate estimates of F, X, and η. Models appropriate to this situation have also been extensively developed by Paulik (1963).

However, even in the multiple-release models the Type II tagging mortality and Type II shedding will generate an underestimate of the true exploitation rate. Thus while the problems imposed by Type I losses may be circumvented by more elaborate experimental designs, the undesired effects of Type II losses remain. Two remedies are possible: 1) The single-tagging may be supplemented with a double-tagging experiment and other special studies to estimate Type II components and determine correction factors, or 2) double-tagging may be used exclusively to estimate mortality rates unaffected by Type I and Type II shedding. Both strategies are treated below. We note here that even when tag shedding and mortality are not the chief concerns of a tagging experiment, double-tagging is often employed simply to increase expected recovery rates (e.g., Hynd 1969; Bayliff 1973).

MODELS OF DOUBLE-TAGGING

We restrict our attention to the case where members of the population are marked with two tags differing in position of attachment and possibly type (call these Type A and Type B). We assume the burden of carrying both tags is equal to the stress of carrying either one alone. Further, we assume that the probabilities of loss are the same for each tag of a specified type and independent of the status of the other tag. Suppose a cohort of fish is double-tagged at time 0. For any fish still alive at time t, the probability that the Type A tag has been shed can be stated as

$$\Omega_A(t) = 1 - \rho_A g_A(t)$$

where $g_A(t) = \exp\left(-\int_0^t L_A(u)\,du\right)$.

An analogous expression exists with respect to tag B. Where shedding rates are assumed to be the same for tag Types A and B the subscripts can be dropped, i.e., the common probability of shedding by time t is

$$\Omega(t) = 1 - \rho g(t). \qquad (2)$$

If we set $L(u) = L$(constant), Equation (2) embodies the assumptions of Bayliff and Mobrand (1972)—Type II shedding is a simple Poisson process with an identical constant rate for each tag, so that each tag has the same probability of shedding by time t. Moreover, in due course all surviving fish will have shed both tags as long as $L > 0$, i.e., $\Omega(\infty) \to 1$.

The validity of this particular set of assumptions has recently been challenged by results of tag-shedding studies with northwest Atlantic bluefin tuna, *Thunnus thynnus*, (Baglin et al. 1980) and with southern bluefin tuna, *T. maccoyii*, (Kirkwood 1981). In the former case, it was found that the Type II shedding rate increased with time. In Kirkwood's analysis it was apparent that the Type II rate decreased markedly over time. Therefore, it clearly would be advantageous to construct a model permitting time-dependent Type II shedding rates. Kirkwood approached this problem by attacking the common assumption of uniform shedding probabilities among all fish in the cohort. Instead, he considered the Type II shedding rate for each tag applied to be constant over time, but further assumed that the rate for each tag was a random variable with specified probability density. In this light, the deterministic model at Equation (2) is replaced by the expectation $J(t) = E[\Omega(t)] = 1 - \rho\, E[g(t)]$. The average time-varying shedding rate at time t may now be defined as

$$\Psi(t) = \frac{E\{g(t) \cdot L\}}{E\{g(t)\}}$$

where the expectations are taken with respect to the probability density of L. Following standard principles of reliability theory, this may be reduced to

$$\Psi(t) = -\frac{\partial \ln E\{g(t)\}}{\partial t}.$$

Under Kirkwood's assumptions $\Psi(t)$ will decrease with time as long as there is variation in shedding rate among tags, i.e., there will be a continuous culling of tags with relatively high shedding probabilities. This concept is clearly an attractive alternative to the Bayliff-Mobrand model.

Problems in which the instantaneous loss rate is treated as a random variable arise in a variety of contexts ranging from bioassay to analysis of labor turnover in corporations. Because of its unimodality and mathematical tractability, the distribution often selected to describe this variation is the gamma distribution with mean λ and variance λ^2/b (e.g., see Bartholomew 1973:186 or McNolty et al. 1980). As Kirkwood (1981) showed, for the tag-shedding problem, this choice leads to

$$J(t) = 1 - \rho\left(\frac{b}{b + \lambda t}\right)^b \qquad (3)$$

so that

$$\Psi(t) = \frac{b\lambda}{b + \lambda t}\,.$$

The Bayliff-Mobrand model is now seen as a special deterministic case; when $b \rightarrow \infty$, $J(t) \rightarrow 1 - \rho\exp(-\lambda t)$ and $\Psi(t) \rightarrow \lambda$. Kirkwood considered a further elaboration of Equation (3) by assuming only a fraction of the tags, δ, will have a nonzero probability of shedding; the remainder are regarded as permanently attached. In this event the expected probability of shedding by time t is

$$J(t) = \delta\left[1 - \rho\left(\frac{b}{b + \lambda t}\right)^b\right]. \qquad (4)$$

While this approach significantly advances the realism and flexibility of tag-shedding theory, it fails to account for the apparent increase in average shedding rate as observed in the Atlantic bluefin tuna. Thus, although permitting variation in shedding rate among tags, it still considers the rate for each tag to be constant over time.

This condition is not apt to hold. As Kirkwood (1981) himself pointed out, plastic dart tags may become so firmly imbedded and overgrown by tissue as time passes that the probability of shedding approaches zero. This is most apt to occur in species which grow slowly, such as the southern bluefin tuna. On the other hand, it is well known that various metallic tags may corrode with time and their shedding probabilities increase. Plastic tags also deteriorate.

Accordingly, consider the Type II shedding rate to be a function of time, $L(t)$. A relatively simple model for this situation is $L(t) = \alpha + \beta t^{(\gamma-1)}$, permitting a wide variety of forms for the instantaneous shedding process. In general, all three parameters of this model could be specified as random variables. Thus with $\alpha > 0$, $\beta > 0$, and $-\infty < \gamma < \infty$ the probability of shedding might increase over time for some fish in a cohort, decrease for others, and be constant for the remainder. However, to simplify the analysis assume here that γ is fixed and identical for all members of the cohort. Now if α and β are independently distributed as gamma random variables we have

$$J(t) = \delta\left[1 - \rho\left(\frac{b}{b + \lambda t}\right)^b\left(\frac{\gamma c}{\gamma c + \xi t^\gamma}\right)^c\right] \qquad (5)$$

and

$$\Psi(t) = \left(\frac{b\lambda}{b + \lambda t}\right) + \left(\frac{\gamma c\ \xi t^{\gamma-1}}{\gamma c + \xi t^\gamma}\right)$$

where the new symbols are ξ, the expected value of β, and c, the reciprocal of the squared coefficient of variation of β. Hence, if between-tag variability in α and β approaches zero,

$$J(t) \rightarrow \delta\left\{1 - \rho\exp\left[-\left(\frac{\lambda t + \xi t^\gamma}{\gamma}\right)\right]\right\}$$

and $\Psi(t) \rightarrow \lambda + \xi t^{(\gamma-1)}$. In the basic model at Equation (4), for tags still in place at time t the conditional probability of shedding in the interval $(t, t + dt)$ is independent of t. In the extended model at Equation (5), this conditional probability may also increase or decrease with t depending on γ.

While elaboration of the tag-shedding equations in this manner is straightforward, it is doubtful whether a very clear discrimination between such parameter-laden models is possible given the usual recapture statistics. Distinctions between the extended models are reduced by the integration of the shedding processes over several recapture periods and are further obscured by sampling variation.

However, on the basis of these conceptual models of the tag-shedding process we can now write the well-known equations describing the expected number of tags of a specified type still attached at time t. For $N_d(0)$ fish initially double-tagged with Types A and B tags, let

$$S(t) = \pi \cdot \exp\left(-\int_0^t Z(u)du\right)$$

be the probability of survival to time t, where $1 - \pi =$ probability of immediate mortality and $Z(u) = H(u) - L(u)$ is the time dependent instantaneous death rate. Then the expected number of fish bearing a single tag of Type A at time t is $N_A(t) = N_d(0)\ S(t)\ J_B(t)(1 - J_A(t))$. An analogous expression may be written for $N_B(t)$, and if the two tags are considered identical, the subscripts A and B may be dropped to yield

$$N_s(t) = N_A(t) + N_B(t)$$

$$= 2N_d(0)\ S(t)\ J(t)\ (1 - J(t)),$$

the expected number of fish still bearing a single tag at time t.

The expected number of double-tagged fish at time t when A and B types are differentiated is $N_d(t) = N_d(0)\ S(t)(1 - J_A(t))(1 - J_B(t))$ or when no distinction is made between A and B types, $N_d(t) = N_d(0)\ S(t)(1 - J(t))^2$. In any event, the total number of fish expected at time t with one or two tags remaining is $N_.(t) = N_s(t) + N_d(t)$.

The processes described above are not directly observable, so inferences about the shedding rates must be made on the basis of catch statistics. When recapture effort is exerted during a time interval we assume it is applied continuously. During a period of length Δ_i beginning at time t_i the expected number of recaptures of tagged fish in category j is therefore

$$E(r_{ji}) = \int_{t_i}^{t_i+\Delta_i} F(u)\ N_j(u)\ du \qquad (6)$$

where $j = \mathrm{A}, \mathrm{B}, s, d, \cdot$.

To complete the integral at Equation (6) it has been customary to make two key assumptions at this juncture (Chapman et al. 1965). First, we assume the fishing mortality rate, $F(u)$, is a step function constant within each recapture interval, i.e., $F(u) = F_i$ for $t_i < u < t_i + \Delta_i$ Second, we assume the average value of $N_j(u)$ during the interval is approximately equal to $N_j(t_i + \Delta_i/2)$. [This approximation is generally quite good for Δ_i of 1 yr or less. If $N_j(u)$ is linear over the interval the relation is exact regardless of Δ_i.] Under these conditions the set of recapture equations becomes

$$E(r_{ji}) = F_i\ \Delta_i\ N_j(\tau_i) \qquad (7)$$

where $\tau_i = t_i + \Delta_i/2$.

The standard procedures for estimating shedding rate parameters, and many of those to be described shortly, rely on a sequence of ratios of the estimated or observed number of recaptures from the various categories during successive fishing periods. It is clear from the equations above that such ratios will be functions of τ_i and the shedding parameters only, and independent of F_i, $N_d(0)$ and any parameters of the survival function $S(\tau_i)$.

Further, the ratios will be unaffected by nonrecovery or nonreturn as long as these processes operate at constant levels with respect to recaptures during a given time interval and at the same rates for each tagged fish category. Throughout this paper we assume this is so. However, this latter condition is one which could be violated easily, particularly if catches are not inspected carefully for tag recaptures. Where fish are handled individually there may be no difference in recovery rates between single- and double-tagged fish. Otherwise, recovery rates may be greater in double-tagged individuals. Once tagged fish are recovered, there may be further problems with respect to return rates. Laurs et al. (1976) in a study of shedding rates in North Pacific albacore, *T. alalunga*, and Myhre (1966) in experiments with Pacific halibut, *Hippoglossus stenolepis*, allowed for the possibility that a certain proportion of double-tagged recoveries would be misreported as having only a single tag. [For example, a fisherman might pocket one of the tags as a souvenir, or one tag might be simply lost after recapture.]

ESTIMATION OF SHEDDING RATES AND PARAMETERS

In the analysis of tag-shedding data a broad range of objectives may be pursued, and these give rise to a variety of estimation problems and approaches. Fundamentally, of course, the analyst wishes to correct systematic bias in estimates of basic population parameters caused by tag loss. There are several ways to do this. Where concurrent single-tagging and double-tagging experiments are conducted, information on shedding rates from the double-tagging may be used to compute adjustment factors, which in turn are applied to recoveries from the primary single-tagging study. Thus in single-tag estimation procedures based on Equation (1), for example, r_i would simply be replaced by

$$r'_i = r_i \, \kappa_i^{-1}, \tag{8}$$

where κ_i, estimated from double-tagging, is the probability that a tag will still be attached at time τ_i. If returns from the double-tagging experiment are too few to provide an estimate of κ_i for each recapture interval, interpolation is necessary. In any event, in this approach only minimal assumptions need be made about the manner in which shedding occurs.

In most treatments of tag shedding, however, a specific model is postulated for the shedding process. Once the parameters of such a model are estimated, appropriate adjustments for tag shedding are made either to the single-tag recovery data, as above, or directly to estimated population parameters. A third strategy is to conduct the experiment entirely with double-tagged fish, and to estimate mortality rates and other population parameters directly, in such a way that no corrections are necessary.

These various approaches are discussed now in greater detail, assuming a continuous recapture process. For situations in which tagged fish are recaptured once at most, but only in point samples, some estimation procedures are given by Seber (1973) and Seber and Felton (1981). For multiple-recapture models of the Jolly-Seber type, again with point sampling, the reader should consult Arnason and Mills (1981).

Estimating Adjustment Factors for Single-Tag Recoveries

Here we estimate κ_i, the probability of tag retention at time τ_i, the midpoint of the ith recapture period. We assume the shedding probabilities for each tag are identical and independent of the status of the other tag, and that recovery and reporting rates are the same for recaptured fish bearing either one tag or two. Under these conditions the number of double-tag recoveries, r_{di}, is proportional to κ_i^2 and the number recovered with only a single tag remaining, r_{si}, is proportional by the same factor to $2\kappa_i(1-\kappa_i)$. Of the total number of recoveries from the double-tagging experiment in the ith period, the proportion bearing two tags is therefore

$$P_{di} = \frac{\kappa_i}{2 - \kappa_i} .$$

Maximum likelihood (ML) estimates of the κ_i are now easily derived. We assume the conditional distribution of r_{di}, given $(r_{di} + r_{si})$, is binomial with parameter P_{di}. The likelihood of the ith recapture sample is thus

$$\mathfrak{L}_i = \left(\frac{r_i!}{r_{di}!\; r_{si}!}\right)\left(\frac{\kappa_i}{2-\kappa_i}\right)^{r_{di}}\left(1 - \frac{\kappa_i}{2-\kappa_i}\right)^{r_{si}} .$$

The ML estimator of κ_i is easily found:

$$\hat{\kappa}_i = \frac{2 r_{di}}{r_{si} + 2 r_{di}} . \tag{9}$$

This result is also given by Seber (1973) under somewhat different assumptions. The asymptotic variance of $\hat{\kappa}_i$ is

$$\sigma^2_{\hat{\kappa}_i} = \frac{\kappa_i (1-\kappa_i)\,(2-\kappa_i)^2}{2 r_{.i}} . \tag{10}$$

As usual, numerical estimates are computed by inserting $\hat{\kappa}_i$ in place of κ_i.

Note that $\hat{\kappa}_i$ has a small negative statistical bias. In fact, using a Taylor series expansion it may be shown that

$$E(\hat{\kappa}_i) \simeq \kappa_i \left[1 - \frac{(1-\kappa_i)\,(2-\kappa_i)}{2 r_{.i}}\right].$$

Bias increases with time out, i.e., as κ_i decreases, and is inversely related to the total number of recaptures. When $\kappa_i = 0.5$ and $r_{.i} = 10$, the negative bias in $\hat{\kappa}_i$ is <4%.

Note further that since the likelihood function is conditioned on $r_{.i}$, inferences based on Equations (9) and (10) apply strictly only to the particular experimental outcome being studied, and not to the broader class of results which might be obtained in replications of the experiment. Providing that the approximation in Equation (7) is valid, a more complicated unconditional model would yield the same estimate of κ_i, but the variance of $\hat{\kappa}_i$ would be greater, reflecting the stochastic nature of the mortality and recapture processes which lead to the $r_{.i}$. Since our interest is in estimating shedding rates and not mortality rates, as a rule we consider only the simpler conditional likelihoods.

Above we have assumed the two tags are identical insofar as shedding rates are concerned. When they are subject to different shedding rates another set of estimators is required. Where A and B tags are identified, the number of A-type recaptures, r_{Ai}, is proportional to $\kappa_{Ai}(1-\kappa_{Bi})$ while r_{Bi} is proportional to $\kappa_{Bi}(1-\kappa_{Ai})$. The number of double-tagged recaptures is proportional to $\kappa_{Ai}\,\kappa_{Bi}$. We assume the number of recaptures in the three classes are trinomial given $r_{Ai}+r_{Bi}+r_{di}$, with conditional probabilities

$$P_{Ai} = \frac{\kappa_{Ai}(1-\kappa_{Bi})}{1-(1-\kappa_{Ai})\,(1-\kappa_{Bi})}$$

$$P_{Bi} = \frac{\kappa_{Bi}(1-\kappa_{Ai})}{1-(1-\kappa_{Ai})\,(1-\kappa_{Bi})}$$

$$P_{di} = \frac{\kappa_{Ai}\,\kappa_{Bi}}{1-(1-\kappa_{Ai})\,(1-\kappa_{Bi})}\,.$$

These assumptions lead to the *ML* estimates

$$\hat{\kappa}_{Ai} = \frac{r_{di}}{r_{Bi}+r_{di}} \quad \text{and} \quad \hat{\kappa}_{Bi} = \frac{r_{di}}{r_{Ai}+r_{di}}\,.$$

Estimating Parameters of Specific Models

Regression Methods

Despite the directness and simplicity of the general adjustment procedure outlined above, most double-tag analyses have aimed at unraveling specific underlying mechanisms of the tag-shedding process. The probability of tag retention, κ_i, is then seen as a continuous function of time and a vector of model parameters, θ, to be estimated from the recapture data. In the terminology established above, $\kappa_i = 1 - J(\tau_i)$. Thus if $\hat{\kappa}_i$ or some transformation of $\hat{\kappa}_i$ is plotted against τ_i the form of an appropriate shedding model may be revealed. In fact, this is the approach adopted in much of the recent tag-shedding literature, and various weighted regression procedures have been developed to handle the parameter estimation. The general formulation of these is: find θ such that

$$S(\theta) = \sum_{i=1}^{n} w_i\,(y_i - f_i(\theta))^2$$

is minimum. In the two-parameter Bayliff-Mobrand model $y_i = \ln\hat{\kappa}_i$, where $\hat{\kappa}_i$ is given in Equation (9), and $f_i(\theta) = \ln\rho - L\tau_i$. In the four-parameter Kirkwood model

$$y_i = 1 - \hat{\kappa}_i$$

and

$$f_i(\theta) = \delta\left\{1 - \rho\left(\frac{b}{b+\lambda\tau_i}\right)^b\right\}.$$

In both cases the authors suggest setting $w_i = r_{.i}$. This is not optimal in a statistical sense, but is clearly preferable to equal weighting. It should be noted further that neither the Bayliff-Mobrand model nor the Kirkwood model is based on an explicit consideration of error structure for the observations. For example, there is considerable support in the literature for a multiplicative error in the recapture process, i.e., $r_{si} = E(r_{si})\exp(\epsilon_{si})$ and $r_{di} = E(r_{di})\exp(\epsilon_{di})$ and in this case the algebra leads one to the nonlinear model

$$\ln\left\{\frac{r_{si}}{2r_{di}}\right\} = \ln\left\{\frac{J(\tau_i)}{1-J(\tau_i)}\right\} + \epsilon_i$$

where ϵ_i has mean 0 and variance $\sigma^2_{\epsilon_i}$. Appropriate weights for this model are

$$w_i = \sigma^{-2}_{\epsilon_i} \simeq \frac{r_{si}\,r_{di}}{r_{.i}}\,.$$

The regression models discussed here have assumed that recaptures are obtained from a single cohort of tagged fish. However, it is often the case that several lots of tagged fish are released at different times, so the recaptures in a particular interval may come from different cohorts. In this event the analysis may be applied to each of the m cohorts separately, provided these are fairly large. When multiple releases are made but the individual cohorts are small, so that relatively few recaptures are expected from each cohort, the usual procedure is to assume mortality rates and shedding rates are constant and identical for each group and to simply aggregate the recapture statistics from the several releases. Let the recapture intervals be of equal length, Δ, and let r_{sij} and r_{dij} denote the number of single-tagged and double-tagged fish from the jth cohort recaptured during the ith interval following that cohort's liberation. Employing the Bayliff-Mobrand linear regression model, one can estimate $\ln\rho$ and L in the usual manner as

$$\hat{\beta} = (X^T\,W\,X)^{-1}\,X^T\,W\,Y \qquad (11)$$

where $\beta = [\ln\rho \;\; L]^T$

$X = \{x_{ij}\}$ is the augmented data matrix such that $x_{i1} = 1$ for all i and $x_{i2} = -(i - 1/2)\,\Delta$

$Y = \{y_i\}$ is the vector of dependent variables with elements

$$y_i = \ln\left\{\frac{2\sum_{j=1}^{m_i} r_{dij}}{\sum_{j=1}^{m_i} r_{sij} + 2\sum_{j=1}^{m_i} r_{dij}}\right\}. \qquad (12)$$

Here W is a matrix of statistical weights, and m_i is the number of cohorts for which recapture statistics are available in the ith postrelease interval. The symbol T denotes the matrix transpose.

If sufficient recaptures are obtained to analyze each cohort separately (say $r_{ij} \geq 10$) but a common shedding rate is assumed, several alternative approaches are available. First we can treat the separate releases as partial replicates of the same experiment and construct the dependent variables as the logarithms of the geometric means of individual statistics for each cohort. Thus to estimate $\ln\rho$ and L we use Equation (11) as before but now set

$$y_i = \sum_{j=1}^{m_i} \ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right)\bigg/ m_i. \qquad (13)$$

Although as an estimator of $\ln\hat{\kappa}_i$ Equation (13) usually has slightly greater negative bias than Equation (12), such bias is negligible and the approach taken in Equation (13) has the advantage that statistical weights may be calculated empirically for cases where $m_i \geq 2$. In particular, define the ith diagonal element of W as

$$w_{ii} = m_i(m_i - 1)\left[\sum_{j=1}^{m_i}\left(\ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right) - y_i\right)^2\right]^{-1}$$

where y_i is given by Equation (13), and let $w_{ij} = 0$ for $i \neq j$. When some of the m_i are equal to 1, then the w_{ii} may be computed using the delta method as

$$w_{ii} = m_i^2\left[\sum_{j=1}^{m_i}\left(\frac{r_{sij}(r_{sij} + r_{dij})}{r_{dij}(r_{sij} + 2r_{dij})^2}\right)\right]^{-1}$$

on the assumption that the r_{dij} and r_{sij} are complementary binomial variables.

A second approach when the shedding rates are constant and the r_{ij} are sufficiently large is to treat returns from each of the m releases separately and then average the individual estimates. Thus the overall estimate of L, for example, would be

$$\hat{L} = \sum_{j=1}^{m} w_j'\,\hat{L}_j$$

where $\hat{L}_j$ is the estimated slope from the linear regression of

$$y_{ij} = \ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right)$$

on τ_i. Here the individual estimate of L from the jth cohort is given a weight w_j' inversely proportional to its relative variance. In practice we substitute the statistic

$$\hat{w}_j' = \frac{\hat{\sigma}_{\hat{L}_j}^{-2}}{\sum_{j=1}^{m} \hat{\sigma}_{\hat{L}_j}^{-2}},$$

$\hat{\sigma}_{\hat{L}_j}^{-2}$ being the estimated variance of L_j computed in the jth regression. For the regression analysis itself, appropriate statistical weights for the y_{ij} would be proportional to

$$\hat{\sigma}_{y_{ij}}^{-2} = \frac{r_{dij}\,(r_{sij} + 2r_{dij})^2}{r_{sij}\,(r_{sij} + r_{dij})}.$$

Finally, the variance of $\hat{L}$ may be estimated as

$$\hat{\sigma}_{\hat{L}}^2 = \sum_{j=1}^{m} \hat{w}_j'^2\,\hat{\sigma}_{\hat{L}_j}^2 = \left[\sum_{j=1}^{m} \hat{\sigma}_{\hat{L}_j}^{-2}\right]^{-1}.$$

A third approach is to assume that the set of regression estimates from the m cohorts are sampled from an underlying but unspecified stochastic process which, with respect to the estimation of Type II shedding rate, has mean L and variance $\sigma_{\hat{L}}^2$. The regressions of y_{ij} on τ_i are unweighted, and empirical estimates of L and $\sigma_{\hat{L}}^2$ are given very simply by

$$\hat{L} = \sum_{j=1}^{m} \hat{L}_j\Big/m$$

and

$$\hat{\sigma}_{\hat{L}}^2 = \sum_{j=1}^{m} (\hat{L}_j - \hat{L})^2\Big/m(m - 1),$$

where $\hat{L}_j$ is the regression estimate corresponding to the jth cohort.

A shortcoming of many double-tag analyses is that attention has been focused on estimating constant ρ and L despite the existence of multiple-release statistics. In fact the multiple-release experiment permits a more elaborate assessment of shedding processes, with the level of detail determined by specific characteristics of the experimental design. To illustrate this, consider an experiment with six recapture periods of equal length, Δ. Two cohorts of double-tagged fish are released, at the beginning of the first and fourth periods. We assume there is a unique Type I shedding rate associated with each cohort, and that the Type II shedding rate is the same for each group but is a function of time following release. Specifically, we assume the latter rate is constant for two recapture intervals following the release of any cohort, may then change to another constant level for two more periods, and so on.

The recapture statistics from the experiment may be arrayed as follows:

	Recapture interval:					
Release group	*1*	*2*	*3*	*4*	*5*	*6*
1	r_{s11} r_{d11}	r_{s12} r_{d12}	r_{s13} r_{d13}	r_{s14} r_{d14}	r_{s15} r_{d15}	r_{s16} r_{d16}
2				r_{s21} r_{d21}	r_{s22} r_{d22}	r_{s23} r_{d23}

Note that $m_1 = m_2 = m_3 = 2$ and $m_4 = m_5 = m_6 = 1$.

The parameter vector $\beta = [\ln\rho_1 \ln\rho_2 \, L_1 \, L_2 \, L_3]^T$ may now be estimated from Equation (11) with Y as given in Equation (13) and the data matrix defined as

$$X = \begin{bmatrix} 1/2 & 1/2 & -\Delta/2 & 0 & 0 \\ 1/2 & 1/2 & -3\Delta/2 & 0 & 0 \\ 1/2 & 1/2 & -2\Delta & -\Delta/2 & 0 \\ 1 & 0 & -2\Delta & -3\Delta/2 & 0 \\ 1 & 0 & -2\Delta & -2\Delta & -\Delta/2 \\ 1 & 0 & -2\Delta & -2\Delta & -3\Delta/2 \end{bmatrix}.$$

As usual, the covariance matrix of $\hat{\beta}$ is estimated by $\hat{V} = (X^T W X)^{-1}$.

With a little imagination this general linear model can easily be adapted to accommodate a wide variety of multiple-release experimental designs. Standard analysis of covariance techniques may be applied to test the associated hypotheses concerning β.

Maximum Likelihood Methods

As an alternative to the least squares methods we now describe some *ML* procedures for estimating the model parameters in the single-release case. Given the total number of recaptures in the ith period we again assume the numbers falling in the various classes are multinomially distributed. Thus when the A and B tags are identical there are just two classes, and the numbers in each are binomial variables with conditional expectations

$$\begin{aligned} E(r_{di}) &= r_{\cdot i} \quad P_{di} \\ &= r_{\cdot i}\left\{\frac{1 - J(\tau_i)}{1 + J(\tau_i)}\right\} \\ &= r_{\cdot i}\left\{\frac{[1 - J(\tau_i)]^2}{1 - J(\tau_i)^2}\right\} \end{aligned}$$

and $E(r_{si}) = r_{\cdot i}\,(1 - P_{di})$. Assuming further that the statistics for successive periods are mutually independent, the joint likelihood function for the double-tag recovery data $\{r_{d1}\; r_{d2}, \ldots, r_{dn}\}$ given $\{r_{\cdot 1}, r_{\cdot 2}, \ldots, r_{\cdot n}\}$ is

$$\mathfrak{L} = \prod_{i=1}^{n} \left(\frac{r_{\cdot i}!}{r_{di}!\; r_{si}!}\right) P_{di}^{\;r_{di}} (1 - P_{di})^{r_{si}} \qquad (14)$$

where P_{di} is a function of τ_i and the vector of parameters to be estimated, θ.

When the A and B tags are not identical, the recaptures are partitioned into three disjoint classes, and the numbers in each are trinomial with expectations

$$E(r_{Ai}) = \frac{J_B(\tau_i)\,(1 - J_A(\tau_i))}{1 - J_B(\tau_i)\,J_A(\tau_i)}\, r_{\cdot i} = r_{\cdot i}\, P_{Ai}$$

$$E(r_{B_i}) = \frac{J_A(\tau_i)\,(1 - J_B(\tau_i))}{1 - J_B(\tau_i)\,J_A(\tau_i)}\, r_{\cdot i} = r_{\cdot i}\, P_{Bi}$$

and

$$\begin{aligned} E(r_{di}) &= \frac{(1 - J_A(\tau_i))\,(1 - J_B(\tau_i))}{1 - J_B(\tau_i)\,J_A(\tau_i)}\, r_{\cdot i} \\ &= r_{\cdot i}\,(1 - P_{Ai} - P_{Bi}). \end{aligned}$$

Now the joint conditional likelihood of the recapture sample is

$$\mathcal{L} = \prod_{i=1}^{n} \left(\frac{r_{\cdot i}!}{r_{Ai}!\; r_{Bi}!\; r_{di}!}\right) P_{Ai}^{\;r_{Ai}}\, P_{Bi}^{\;r_{Bi}} \times (1 - P_{Ai} - P_{Bi})^{r_{di}}.$$

In either case, once the underlying model and the corresponding elements of θ are identified, the ML estimates of θ may be computed by maximizing $\mathcal{L}$ directly using a variety of iterative search procedures. In some situations the derivatives of $\mathcal{L}$ with respect to θ are easily derived, but even then only numerical solutions are possible.

For example, when A and B tags are identical and $J(\tau_i) = 1 - \rho(\exp(-L\tau_i))$, the ML estimates of ρ and L are found by solving the system of equations

$$0 = \sum_{i=1}^{n} \tau_i\, C_i \quad \text{and} \quad 0 = \sum_{i=1}^{n} C_i$$

$$\text{where } C_i = \frac{(1 + P_{di})\,(r_{di} - P_{di}\, r_{\cdot i})}{1 - P_{di}}$$

$$= J(\tau_i)^{-1}\left\{r_{di} - r_{\cdot i}\left(\frac{1 - J(\tau_i)}{1 + J(\tau_i)}\right)\right\}$$

$$= J(\tau_i)^{-1}\{r_{di} - E(r_{di})\}.$$

The asymptotic covariance matrix of $\hat{L}$ and $\hat{\rho}$ may then be derived in the usual manner by inverting the corresponding negative information matrix

$$I = \begin{bmatrix} \sum_{i=1}^{n} \tau_i^2\, D_i & -\frac{1}{\rho}\sum_{i=1}^{n} \tau_i\, D_i \\ -\frac{1}{\rho}\sum_{i=1}^{n} \tau_i\, D_i & \frac{1}{\rho^2}\sum_{i=1}^{n} D_i \end{bmatrix}$$

$$\text{where } D_i = \frac{r_{\cdot i}\, P_{di}\,(1 + P_{di})^2}{1 - P_{di}}.$$

Explicit analytical solutions are possible when there is only a single recapture period centered at τ and the model is reduced to a one-parameter function of either the Type I or Type II shedding rate, i.e., either $J(\tau) = 1 - \exp(-L\tau)$ or $J(\tau) = 1 - \rho$. In this event the ML estimate of L (with $\rho = 1$) is

$$\hat{L} = -\frac{1}{\tau}\ln\left\{\frac{2r_d}{r_s + 2r_d}\right\} \qquad (15)$$

with asymptotic variance estimated by

$$\hat{\sigma}^2_{\hat{L}} = \frac{r_s\,(r_s + r_d)}{\tau^2 r_d\,(r_s + 2r_d)^2},$$

or when shedding is a function of ρ only (with $L = 0$)

$$\hat{\rho} = \frac{2r_d}{r_s + 2r_d} \qquad (16)$$

and

$$\hat{\sigma}^2_{\hat{\rho}} = \frac{r_s\, 2r_d}{(r_s + 2r_d)^3}.$$

In the case of identical A and B tags a convenient alternative to direct maximization of the likelihood function is to fit the recapture data to their expectations using an iteratively reweighted Gauss-Newton algorithm. To accomplish this one may use routines available in certain standard statistical software packages, e.g., BMDP[2]. Specifically, we find an admissible value of θ which minimizes the sum of squares

$$S' = \sum_{i=1}^{n} w_i[r_{di} - E(r_{di})]^2.$$

Since the r_{di} are assumed to be binomial (i.e., of "regular exponential" form), minimizing S' with a Gauss-Newton routine is equivalent to maximizing the likelihood of Equation (14) provided the weights used are the reciprocals of the variances of the r_{di} and are recomputed at each iteration based on the current parameter values (Wedderburn 1974; Jennrich and Moore 1975; Jennrich and Ralston 1978). In this case the weights must be $\tilde{w}_i = [r_{\cdot i}\, \tilde{P}_{di}\,(1 - \tilde{P}_{di})]^{-1}$, where $\tilde{P}_{di}$ is the function P_{di} evaluated at the current parameter estimates. Asymptotic standard errors for the parameter estimates are also computed by the BMDP routine.

A similar device may be used when a distinction is made between A and B tags. Given $r_{Ai} + r_{di}$ we assume r_{di} is binomial with expectation $E_B(r_{di}) = (r_{Ai} + r_{di})\,(1 - J_B(\tau_i))$. Analogously,

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

$E_{\mathrm{A}}(r_{di}) = (r_{\mathrm{B}i} + r_{di})\,(1 - J_{\mathrm{A}}(\tau_i))$. Thus an iteratively reweighted Gauss-Newton algorithm minimizing

$$S'_{\mathrm{B}} = \sum_{i=1}^{n} w_{\mathrm{B}i}\,(r_{di} - E_{\mathrm{B}}(r_{di}))^2$$

with $w_{\mathrm{B}i} = \tilde{w}_{\mathrm{B}i} = [(r_{\mathrm{A}i} + r_{di})\,\tilde{J}_{\mathrm{B}}(\tau_i)(1 - \tilde{J}_{\mathrm{B}}(\tau_i))]^{-1}$ is used to compute *ML* estimates of shedding parameters for the B class of tags. A parallel procedure gives *ML* estimates of parameters for the A class. Note that the two sets of parameter estimates are not independent.

Unknown Recapture Times

A tacit assumption in the foregoing procedures is that the time between release and recapture for each returned fish is known to "interval accuracy," and that exact recapture time information is available for only a fraction of the recoveries, so that all recoveries are grouped into the n time intervals to permit estimation. This will often be the case. However, in some fisheries it is conceivable that only the crudest sort of information is available on recapture times. For estimation purposes, all that is known is r_d and r_s, the total number of recaptures in each class over the experimental period $(0, T)$. When T is relatively small, say 1 yr or less, then estimation of a single Type I or Type II shedding parameter is possible, as in Equation (15) or (16). In an experiment of longer duration this is not feasible. However, it is possible under certain circumstances to estimate the ratio of the Type II shedding rate to other Type II losses. Let fishing be constant, continuous, and uniform at an instantaneous rate F. Assume further that the total instantaneous mortality rate is a constant, Z, and that shedding of tags occurs at an instantaneous rate L. If there are no Type I losses, the ratio of $E(r_s)$ to $E(r_d)$ in a double-tagging experiment approaches

$$x = \frac{2L}{Z + L}$$

as $T \rightarrow \infty$. Thus if $L = aZ$, a moment estimator of a is provided by

$$\hat{a} = \frac{\hat{x}}{2 - \hat{x}}$$

$$= \frac{r_s}{2r_d - r_s}, \quad 0 \leq \frac{r_s}{r_d} < 2 \qquad (17)$$

and if one has an estimate of Z which has a systematic bias due to Type II shedding, say Z^{+}, then a corrected estimate may be obtained, i.e., $Z^{*} = Z^{+}(1 + \hat{a})^{-1}$.

This method may also be used where single-tagging and double-tagging experiments are run concurrently. Then if $N_d(0)$ fish are released double-tagged and $N_s(0)$ with single tags, let r'_d and r'_s be recaptures from each group still bearing the initial complement of tags. Under the same assumptions as above this leads to

$$\hat{a} = \frac{r'_s N_d(0) - r'_d N_s(0)}{2r'_d N_s(0) - r'_s \mathrm{N}_d(0)}, \quad 1 \leq \frac{r'_s N_d(0)}{r'_d N_s(0)} < 2.$$

Exact Recapture Times

Turning now to the other end of the spectrum, under ideal conditions it is possible that the exact time out will be known for each fish returned. When exact recapture times are available for all fish the returns from a single-tagging experiment may be analyzed using *ML* procedures first developed by Gulland (1955) and later elaborated by Chapman (1961) and Paulik (1963). These rest on the assumption of binomial recapture probabilities based on constant Type II loss rates and on a resulting conditional recapture time distribution which is truncated negative exponential. Chapman et al. (1965) extended the same concepts to returns of fish initially double-tagged and still retaining both tags upon recapture, and showed that the difference between the estimated total Type II loss rate in a double-tagging experiment and the corresponding total Type II loss rate in a single-tagging study yielded an estimate of L. They noted that this is the best estimate of L possible using only the recapture information from a single-tagging experiment and from fish put out and returned with two tags. Left open was the possibility of combining this information with recapture times for fish initially double-tagged but returned with only one tag still attached. For this class of fish the distribution of recapture times is more complicated.

We now consider an exact recapture time model for an experiment based exclusively on fish initially double-tagged. Suppose $N'_d(0)$ double-tagged fish are released at time 0. Over the course of the experiment, terminating at time T, a total of r_d fish are recaptured and returned with both tags intact, and r_s with only a single tag remaining. In addition, for each tagged fish returned we assume the exact recapture time is known, i.e., we know $\{t_{s1}, t_{s2}, ..., t_{sr_s}\}$ and $\{t_{d1}, t_{d2}, ..., t_{dr_d}\}$.

Let $\Phi_d = Pr$ {fish is returned with both tags intact in (0, T)} and $\Phi_s = Pr$ {fish is returned with one tag remaining in (0, T)}. Then, assuming independence between fish and between the two tags initially applied, the numbers of returns in the various classes are trinomial random variables, i.e.,

$$Pr\{r_d, r_s\} = \frac{N_d(0)!}{r_d!\ r_s!\ (N_d(0) - r_d - r_s)!} \times \Phi_s^{r_s}\ \Phi_d^{r_d} (1 - \Phi_s\ \Phi_d)^{N_d(0) - r_s - r_d}.$$

Following principles set out previously we write the recapture probabilities as

$$\Phi_s = 2 \int_0^T F(u)\ S(u)\ J(u)\ (1 - J(u))\ du$$

and

$$\Phi_d = \int_0^T F(u)\ S(u)\ (1 - J(u))^2\ du.$$

Further, the conditional probability densities for recapture times are

$$f_s(t) = \begin{cases} 2F(t)\ S(t)\ J(t)(1 - J(t))/\Phi_s & 0 < t < T \\ 0 & \text{otherwise} \end{cases}$$

$$f_d(t) = \begin{cases} F(t)\ S(t)(1 - J(t))^2/\Phi_d & 0 < t < T \\ 0 & \text{otherwise.} \end{cases}$$

The joint likelihood function for the observed numbers of single- and double-tag recoveries and the respective sets of recapture times may now be written as

$$\mathfrak{L} = Pr\{r_d, r_s\} \prod_{i=1}^{r_s} f_s(t_{si}) \prod_{i=1}^{r_d} f_d(t_{di}).$$

For specified forms of $F(u)$, $S(u)$, and $J(u)$ computation of ML estimates may now be contemplated, although the form of $\mathfrak{L}$ is apt to be exceedingly complex in most situations. For example, taking the most elementary case, assume that $J(u) = 1 - \exp(-Lu)$, $S(u) = \exp[-(M + F)u]$ and $F(u) = F$ for $0 < u < T$. Also let $T \rightarrow \infty$. Under these conditions the log-likelihood becomes

$$\ln \mathfrak{L} = \mathrm{K} + r_.\ \ln F + (N_d(0) - r_.) \times \ln\left(1 - \frac{2LF^2}{(F + M + L)(F + M + 2L)^2}\right) - (F + M)\ T_. - L(T_s + 2T_d) + \sum_{i=1}^{r_s} \ln(1 - \exp(-Lt_{si}))$$

where K is a function of the observations only,

$$T_s = \sum_{i=1}^{r_s} t_{si}, \qquad T_d = \sum_{i=1}^{r_d} t_{di},$$

$$T_. = T_s + T_d, \quad \text{and} \quad r_. = r_s + r_d.$$

Using numerical methods this may now be maximized as a function of F, M, and L in the usual manner to yield ML estimates of these parameters, as well as asymptotic variance estimates.

A simpler approach which yields information on $Z = F + M$ and L is to condition the likelihood of r_d and r_s on the total number of recaptures, $r_.$, i.e.,

$$Pr\ \{r_d, r_s\} = \left(\frac{r_.!}{r_s!\ r_d!}\right)\left(\frac{\Phi_s}{\Phi_s + \Phi_d}\right)^{r_s}\left(\frac{\Phi_d}{\Phi_s + \Phi_d}\right)^{r_d}.$$

This gives the log-likelihood

$$\ln \mathfrak{L} = \mathrm{K}' + r_.\ \{\ln(Z + L) + \ln(Z + 2L) - \ln(Z + 3L)\} - ZT_. - L(T_. + T_d) + \sum_{i=1}^{r_s} \ln(1 - \exp(-Lt_{si})) \qquad (18)$$

where K′ is independent of Z and L.

Differentiating Equation (18) with respect to Z and L and setting the derivatives to zero one finds that the ML estimates of Z and L satisfy, among other relations, the equation

$$\frac{T_.}{r_.} = \frac{1}{Z + L} + \frac{1}{Z + 2L} - \frac{1}{Z + 3L}.$$

Combining this with the result at Equation (17) leads immediately to a solution for $\hat{Z}$, i.e.,

$$\hat{Z} = \frac{r_{\cdot}}{T_{\cdot}}\left[\frac{1}{1+\hat{a}} + \frac{1}{1+2\hat{a}} - \frac{1}{1+3\hat{a}}\right]$$

whence $\hat{L} = \hat{a}\,\hat{Z}$.

Estimating Mortality Rates by Double-Tagging All Fish

In most of the preceding sections we assumed the basic purpose in double-tagging was to provide auxilliary information on shedding rates which could then be applied to correct recapture statistics or mortality rate estimates obtained in a primary single-tagging experiment. An attractive alternative is to use double-tagged fish entirely and to estimate the mortality rates and other vital parameters in such a way that no bias corrections are necessary. If exact recapture times are recorded, the *ML* model just discussed is appropriate. When recapture data are grouped into n time intervals of length Δ_i centered at times τ_i, a convenient context for developing this approach is the single-tagging regression model suggested by Chapman (1961) and discussed further by Cormack (1968) and Seber (1973). This takes the form

$$\ln\left(\frac{r_i}{\mathfrak{f}_i\,\Delta_i}\right) = \ln[q\rho N_s(0)] - q\mathfrak{f}_i' - X\tau_i + e_i \quad (19)$$

where $\mathfrak{f}_i$ = the nominal fishing effort during period i

$\mathfrak{f}_i' = \sum_{j=1}^{i-1} \mathfrak{f}_j\,\Delta_j + \frac{\mathfrak{f}_i\,\Delta_i}{2}$ = the estimated nominal effort up to time τ_i

q = the catchability coefficient

e_i = a random error term.

In this particular model one obtains estimates of q and X, and, since $N_s(0)$ is known, an estimate of ρ as well. However, in the presence of Type II shedding the exploitation rate for any period will be underestimated, i.e., hidden in $\hat{X}$ will be the term L. The usual procedure would be to correct $\hat{X}$ by subtracting $\hat{L}$, where $\hat{L}$ is obtained in an independent double-tagging experiment. Instead, if we apply the model directly to recapture statistics from a double-tagging experiment ($N_d(0)$ fish initially double-tagged) we will obtain an estimate of X unaffected by Type II losses and in need of no corrections. This is accomplished by substituting the dependent variable

$$\ln\left\{\left(\frac{r_{si} + 2r_{di}}{2\Delta_i\,\mathfrak{f}_i}\right)\Big/\left(\frac{2r_{di}}{r_{si} + 2r_{di}}\right)\right\}. \quad (20)$$

Further, it now transpires that the estimate of the regression intercept term is free of Type I shedding effects, i.e., one will estimate $\ln[qN_d(0)]$ rather than $\ln[q\rho N_d(0)]$.

If we assume r_{si} and r_{di} are complementary binomial variables given $r_{\cdot i}$, and that $r_{\cdot i}$ is Poisson, then approximately correct weights for the regression employing Equation (20) are

$$w_i = \left[\frac{1}{r_{\cdot i}}\left(1 + \frac{r_{si}^3}{(r_{si} + 2r_{di})^2\,r_{di}}\right)\right]^{-1}.$$

When effort statistics are not available so that a constant fishing mortality rate must be assumed, or when there is a linear dependence between the two independent variables $\mathfrak{f}_i'$ and τ_i, then separate estimates of q and X are not possible using the single-tag model of Equation (19) unless Type I errors are absent. Nor is ρ estimable. Instead, one may only regress $\ln(r_i/\Delta_i)$ on τ_i to yield estimates of $\ln[\rho F N_s(0)]$ and $(F+X)$. But when the model is applied to a double-tagging experiment under the same restrictions, it is still possible to estimate both q and X unaffected by shedding.

Note that the dependent variable of Equation (20) from the double-tagging experiment is analogous to the one of Equation (19) appropriately corrected for tag shedding, as in Equation (8). In both cases the recaptures r_{di} and r_{si} are assumed to be point samples taken exactly at τ_i. Thus while in the example above $\kappa_i = \rho\exp(-L\tau_i)$, the correction procedure of Equation (8) and the method outlined here are independent of assumptions on the manner of tag shedding (cf. Seber 1973:281), provided the recapture intervals are reasonably small (say 1 yr or less).

SUMMARY AND CONCLUSIONS

The aim of this paper has been to extend the theory and methodology of estimating tag-shedding rates through double-tagging. Attention was focused on the situation most commonly encountered in fishery applications, wherein two identical tags are placed on each member of an experimental cohort, tagged fish are recaptured at most once in a fishery which is essentially continuous, and the time at liberty is known exactly for only a fraction of the recapture sample.

The regression models studied by Chapman et al. (1965), Bayliff and Mobrand (1972), and Kirkwood (1981) were extended to permit the Type II shedding rate for each tagged fish to be a function of time. Both deterministic and stochastic versions were presented and previously published models were shown to be special cases.

If all tags are subject to the risk of shedding, i.e., if $\delta = 1$, and if data are available from several recapture periods, a simple plot of $\ln\hat{\kappa}_i$ against τ_i will reveal whether the average Type II shedding rate, $\Psi(t)$, is constant; if it is, the relationship will be linear. In this event the most parsimonious model consistent with the data will be the deterministic model based on a constant Type II shedding rate, L. In addition, if the points suggest a negative intercept on the ordinate the Type I retention rate, ρ, may be added to the parameter set. One may then carry out the parameter estimation using either the Bayliff-Mobrand linear regression model, or the nonlinear regression of $\ln(r_{si}/2r_{di})$ on τ_i, depending on which error structure is assumed. However, since the plot of $\ln\hat{\kappa}_i$ versus τ_i is approximately linear even with multiplicative error in the recapture process, it probably makes little difference which estimation method is used as long as proper statistical weights are incorporated.

If $\delta = 1$ and the plot of $\ln\hat{\kappa}_i$ versus τ_i is nonlinear, one of the more complicated tag-shedding models is called for. A trend which is concave downward suggests that $\Psi(t)$ is increasing with time and points to the stochastic model of Equation (5) or its deterministic counterpart. On the other hand, upward concavity could be explained either by a model in which the Type II shedding rate decreased with time or by Kirkwood's (1981) hypothesis, or by a combination of the two as in Equation (5).

Another useful diagnostic plot is $1 - \kappa_i$ against τ_i. These are the variables considered in Kirkwood's nonlinear model. When L is constant the plotted points will be traced by a line analogous to a von Bertalanffy growth curve with asymptote δ and location parameter ρ, and they should indicate which of these two parameters to include in the model and how much precision to expect in the resulting estimates. (In passing, it is worth mentioning that if δ is to be estimated jointly with L, a longer experiment is required to ensure high precision in the parameter estimates than if L alone is being estimated.)

The treatment of recaptures from double-tagging experiments with multiple cohorts was discussed in the context of the Bayliff-Mobrand model. Alternative methods of combining information from several cohorts to estimate common shedding parameters were proposed, and a general linear model approach was suggested for situations where more elaborate structural assumptions are made. A full numerical evaluation of these procedures remains to be done.

As an alternative to the least squares regression methods usually employed, some new *ML* procedures were presented. These are more difficult to use than the regression techniques, but offer advantages in some situations. For example, when only two recapture periods are possible one cannot compute the precision of regression estimates in the Bayliff-Mobrand model, but standard errors in the equivalent *ML* model are still estimable. The most promising method for deriving *ML* estimates in the general case may be the iteratively reweighted Gauss-Newton algorithm. Indeed, if one has access to the right computer software (such as the BMDPAR and BMDP3R programs supplied by BMDP) this approach is nearly as easy to use as the simple Bayliff-Mobrand linear regression method. A sensible procedure would be to first study the diagnostic plots suggested above for the regression analysis, and then fit the selected model using an iteratively reweighted least squares algorithm.

The estimation procedures discussed above are applicable when data are grouped by recapture interval. For situations in which the exact time at liberty is known for each recapture an unconditional *ML* model was developed. This may be applied not only to estimate shedding rates but also to estimate mortality rates unaffected by shedding. However, in its general form the likelihood function is rather complicated and only numerical solutions would be possible in most situations. Analytical estimators for L and Z were derived for a simplified conditional likelihood. Besides the more stringent data requirements this model requires the extra assumption of constant mortality rates during the experiment.

In the final section it was shown that through double-tagging it is possible to estimate mortality rates free of tag-shedding biases even when the recapture data are available only to interval-accuracy, and without resort to the usual concurrent single-tagging experiment. The model was developed in the simple context of a fixed Type II shedding rate, but the principle applies to more complicated shedding processes as well. If the burden imposed by the second tag can be neglected, it therefore seems advantageous to double-tag all fish. In any case, when shedding is appreciable the greater overall recovery rates from double-tagging make the exclusive use of double-tagged fish a proposition well worth considering.

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NOAA, National Marine Fisheries Service
SWFC Honolulu Laboratory F/SWC2
2570 Dole Street
Honolulu, HI 96822-2396